Bulletin
of the
Torrey Botanical Club

VOLUME 62

BRITTON MEMORIAL VOLUME

FOUNDED BY WILLIAM HENRY LEGGETT 1870

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NEW YORK
1935

Published for the Club
GEORGE BANTA PUBLISHING COMPANY
Menasha, Wisconsin

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No. 3, for March, pages 117–176, issued March 1, 1935
No. 4, for April, pages 177–242, issued April 1, 1935
No. 5, for May, pages 243–300, issued May 1, 1935
No. 6, for June, pages 301–368, issued June 1, 1935
No. 7, for October, pages 369–432, issued October 1, 1935
No. 8, for November, pages 433–502, issued November 1, 1935
No. 9, for December, pages 503–565, issued December 10, 1935

The published work of Elizabeth Gertrude Britton[1]

John Hendley Barnhart

Elizabeth Gertrude Knight was born in the city of New York, 9 January 1858. Much of her childhood was spent in Cuba, but she attended school in New York, and was graduated from the Normal College there, now Hunter College, in 1875, and taught in that institution for the next ten years. She became the wife of Nathaniel Lord Britton 27 August 1885, and nearly fifty years later, 25 February 1934, she died at her home near the New York Botanical Garden. Such are the outstanding dates in the life of one who was for more than 54 years an active member of the Torrey Botanical Club, in whose publications many of her papers made their appearance.

Her life has been discussed so well by Marshall A. Howe in the Journal of the New York Botanical Garden (**35**: 97–103, with a portrait. My 1934), that it would be superfluous to repeat essentially the same data here. But it is eminently appropriate that a full statement of her published work should be placed on record in this Bulletin, to whose pages she was long a frequent contributor, and of which she was editor during 1886, 1887, and 1888.

Mrs. Britton was for years the foremost American bryologist, and to most people her name recalled only her studies of mosses; but she was also interested in ferns and flowering plants, and in later years devoted much time to efforts for the preservation of wild flowers. The titles in the accompanying bibliography may be classified roughly as follows:

Mosses	170
Ferns	16
Flowering plants	15
Wild-flower preservation	47
Biography	4
Reviews	66
Miscellaneous	28
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At first it was intended to include no reviews in this list except the many in which valuable original observations were recorded, but it proved so difficult to draw the line that eventually all reviews were included that

[1] Note. It was a request of the late Doctor N. L. Britton that this bibliography be prepared and published in the Bulletin. It is proposed to issue in the near future a Britton Memorial number of the Bulletin.—Editor.

she regarded as of sufficient importance to sign with her name or initials. No doubt she actually wrote many anonymous book-notices, especially during her editorship of the BULLETIN, but the present list is believed to be a virtually complete one of the publications identifiable as her work.

1881

1. Albinism. Bull. Torrey Club **8**: 125. N 1881.

1883

2. Submersed leaves in *Limnanthemum*. Bull. Torrey Club **10**: 34. Mr 1883.
3. On the fruit of *Eustichium norvegicum* Br. Eur. Bull. Torrey Club **10**: 99, 100. *f. 1–6*. S 1883.

1884

4. Note on *Corema Conradii*. Bull. Torrey Club **11**: 116. O 1884.
5. *Salisburia adiantifolia* Smith. Bull. Torrey Club **11**: 134. D 1884.

1886

6. Additions to the Westchester County flora. Bull. Torrey Club **13**: 6, 7. Ja 1886.
7. Botanical notes in the great valley of Virginia and in the southern Alleghanies. Bull. Torrey Club **13**: 69–76. My 1886.
8. Pluralities of embryos in *Quercus alba*. Bull. Torrey Club **13**: 95. *f. 1–3*. Je 1886.

1887

9. Elongation of the inflorescence in *Liquidambar*. Bull. Torrey Club **14**: 95, 96. My 1887.
10. [*Wistaria* at New Dorp, Staten Island.] Bull. Torrey Club **14**: 208, 209. S 1887.

1888

11. [Review of] *Ulota phyllantha* Bridel, La fructification de.—F. Renauld, J. Cardot. Bull. Torrey Club **15**: 203. 2 Jl 1888.
12. *Hypnum* (*Thuidium*) *calyptratum*. Bull. Torrey Club **15**: 220. 2 Au 1888.
13. *Ulota phyllantha* in fruit from Killarney. Jour. Bot. **26**: 282. S 1888.
14. An enumeration of the plants collected by Dr. H. H. Rusby in South America. 1885–1886. —III Pteridophyta. Bull. Torrey Club **15**: 247–253. 3 O 1888.
    Also as a separate, with double pagination, 247–253 and 29–35; included in: Contr. Herb. Columbia Coll. no. 6.
15. [Review of] General index to the first twenty volumes of the Journal (Botany) and the botanical portion of the Proceedings, Nov., 1838, to June, 1886, of the Linnaean [Linnean] Society. Bull. Torrey Club **15**: 268. 3 O 1888.

1889

16. [Review of] The III and IV decades of American Hepaticae [by Lucien Marcus Underwood and Orator Fuller Cook]. Bull. Torrey Club **16**: 79. 8 Mr 1889.
17. Contributions to American bryology.—I. Bull. Torrey Club **16**: 106–112. *pl. 91*. 8 Ap 1889.
    An enumeration of mosses collected by Mr. John B. Leiberg, in Kootenai Co., Idaho.
    Also as a separate: Contr. Herb. Columbia Coll. no. 10.
18. [Review of] Hepaticae, Westindische. F. Stephani. Bull. Torrey Club **16**: 120. 8 Ap 1889.
19. [Review of] Mosses found at Ottawa.—Description[s] of new species of—N. C. Kindberg. Bull. Torrey Club **16**: 141. 8 My 1889.
20. [Review of] Neue Beiträge zur Moosflora von Neu-Guinea.—Von Adelbert [Adalbert] Geheeb. Bull. Torrey Club **16**: 167. 8 Je 1889.
21. *Grimmia torquata* Horns. fertile. Rev. Bryol. **16**: 38, 39. [Je] 1889.
22. [Review of] Kansas fungi. Kellerman and Swingle. Bull. Torrey Club **16**: 196. 6 Jl 1889.
23. *Cladosporium epibryum* Cooke and Massee. Bull. Torrey Club **16**: 225, 226. 1 Au 1889.
24. Peristome of *Grimmia torquata* Hornsch. Rev. Bryol. **16**: 64. [Au] 1889.
25. Germination of lichens on moss protonema. Bull. Torrey Club **16**: 248–250. 19 S 1899.
    Review of "Germination des Lichens sur les protonémas des Mousses," by Gaston Eugène Marie Bonnier (Rev. Gén. Bot. **1**: 165–169. *pl. 8*).

26. [Review of] Canadian mosses. J. Macoun. [Fourth century.] Bull. Torrey Club **16:** 306, 307. 8 N 1889.
27. [Review of] British moss-flora. R. Braithwaite. Part XII. Bull. Torrey Club **16:** 331, 332. 10 D 1889.

1890

28. [Review of] Sur la présence en Anjou de l'*Equisetum littorale* Kuhlwein, par M. l'abbé Hy. Bull. Torrey Club **17:** 17, 18. 15 Ja 1890.
29. [Review of] Fern flora of Canada. George Lawson. Bull. Torrey Club **17:** 21. 15 Ja 1890.
30. [Review of] Ghiesbreght—Explorador de Mexico—Jose N. Roriosa [Rovirosa]. Bull. Torrey Club **17:** 21, 22. 15 Ja 1890.
31. [Review of] Sur les procédés employés par les Japonais pour obtenis des arbres nains; par M. P. Maury. Bull. Torrey Club **17:** 40. 5 F 1890.
32. [Review of] Les plantes aquatiques alimentaires. A. Paillieux et D. Bois. Bull. Torrey Club **17:** 40, 41. 5 F 1890.
33. Hybrid grimmias. Bull. Torrey Club **17:** 157, 158. 9 Je 1890.
34. [Review of] Laboulbeniaceae.—On some North American species of. Roland Thaxter. Bull. Torrey Club **17:** 165. 9 Je 1890.
35. [Criticism of] New mosses of North America. III–IV. Renauld and Cardot. Bot. Gaz. **15:** 151. Je 1890.
36. [Review of] *Tuomeya fluviatilis* Harvey—Concerning the structure and development of. Wm. A. Setchell. Bull. Torrey Club **17:** 189. 1 Jl 1890.
37. [Review of] Collemaceae and allied groups—On the carpologic structure and development of the. Wm. C. Sturgis. Bull. Torrey Club **17:** 181, 182. 1 Jl 1890.
38. [Review of] Artificial keys to the genera and species of mosses recognized in Lesquereux and James' Manual of the mosses of North America. Chas. R. Barnes. Bull. Torrey Club **17:** 180, 181. 1 Jl 1890.
39. Preliminary list of the mosses of Staten Island. [1–4.] Jl 1890.
    Proc. Nat. Sci. Assoc. Staten Isl., special no. 10.
40. [Review of] Mosses—New Canadian. N. C. Kindberg. Bull. Torrey Club **17:** 222. 12 Au 1890.
41. A handbook of the mosses of northeastern America. Bull. Torrey Club **17:** 260. 9 O 1890.
    Announcement of a proposed work that was never published.
42. [Review of] Hépatiques nouvelles des colonies françaises. E. Bescherelle et Richard Spence [Spruce]. Bull. Torrey Club **17:** 266. 9 O 1890.
43. [Review of] Hepaticae novae americanae tropicae et aliae. Richard Spruce. Bull Torrey Club **17:** 266. 9 O 1890.
44. [Review of] North American Sphagna—Contributions to the knowledge of. C. Warnstorf. Bull. Torrey Club **17:** 296. 9 N 1890.
45. [Review of] Hepaticae britannicae exsiccatae, Carrington and Pearson; Fas. IV. Bull. Torrey Club **17:** 319. 9 D 1890.
    Not signed, but authorship indicated in volume-index.
46. List of the mosses collected [in southwestern Virginia]. Mem. Torrey Club **2:** 52, 53. 23 D 1890.

1891

47. [Review of] British moss flora, II. Part XIII. R. Braithwaite. Bull. Torrey Club **18:** 24, 25. 20 Ja 1891.
48. [Review of] Hepaticae—List of Canadian. W. H. Pearson. Bull. Torrey Club **18:** 28, 29. 20 Ja 1891.
49. Contributions to American bryology.—II. Bull. Torrey Club **18:** 49–56. *pl. 114.* 12 F 1891.
    A supplementary enumeration of the mosses collected by Mr. John B. Leiberg in Idaho, with descriptions of two new species.
    Also as a separate: Contr. Herb. Columbia Coll. no. 18.
50. [Review of] Key to the genera and species of British mosses. Rev. H. G. Jameson. Bull. Torrey Club **18:** 128, 129. 4 Ap 1891.
51. [Review of] Vorläufige Mittheilungen über die von mir im Jahre 1888 in Nord Amerika gesammelten neuen Arten und Varietäten der Laubmoose, von Dr. Julius Röll. Bull. Torrey Club **18:** 165. 1 My 1891.

52. [Review of] Hepaticae americanae, L. M. Underwood and O. F. Cook. [Decades IX–X.] Bull. Torrey Club 18: 216. 1 Jl 1891.

1892

53. [Review of] An enumeration of all the species of Musci and Hepaticae recorded from Japan. Wm. Mitten. Bull. Torrey Club 19: 24. 15 Ja 1892.
54. [Review of] Canadian Hepaticae, named by W. H. Pearson, of Manchester, collected and distributed by John Macoun. Bull. Torrey Club 19: 97. 5 Mr 1892.
55. [Review of] *Fontinalis.*—Tableau méthodique et clef dichotomique du genre. J. Cardot. Bull. Torrey Club 19: 98, 99. 5 Mr 1892.
56. [Review of] Hepaticae americanae. Prepared by L. M. Underwood and O. F. Cook. [Decades XI–XII.] Bull. Torrey Club 19: 99. 5 Mr 1892.
57. [Review of] Hepaticae—An arrangement of the genera of. By A. W. Evans. Bull. Torrey Club 19: 99, 100. 5 Mr 1892.
58. [Review of] Mosses—Some new species from the Pribylof Islands, Behring Sea. Collected by Jas. M. Macoun. N. C. Kindberg. Bull. Torrey Club 19: 100. 5 Mr 1892.
59. [Review of] Mosses from Behring Sea, collected by Jas. M. Macoun. N. C. Kindberg. Bull. Torrey Club 19: 100. 5 Mr 1892.
60. [Review of] Mosses of Lancaster County, Pennsylvania—Preliminary list of. J. K. Small. Bull. Torrey Club 19: 135. 5 Ap 1892.
61. [Review of] *Orthotrichum* de l'Amérique—De quelques formes [d']. Venturi. Bull. Torrey Club 19: 165. 5 My 1892.
62. [Review of] Outlines of lessons in botany—Jane H. Newell. Bull. Torrey Club 19: 165, 166. 5 My 1892.
63. [Review of] *Ulota americana* Mitten. F. Venturi. Bull. Torrey Club 19: 169, 170. 5 My 1892.
64. *Leucobryum minus* Hampe. Bull. Torrey Club 19: 189–191. 4 Je 1892.
65. [Review of] Étude sur le genre *Eustichia* (Brid.) C. Mueller. Emile Bescherelle. Bull. Torrey Club 19: 257. 10 Au 1892.
66. [Review of] Plants of the Pribilof Islands, Behring Sea. C. Hart Merriam. Bull. Torrey Club 19: 260, 261. 10 Au 1892.
67. Nomenclator bryologicus. Bull. Torrey Club 19: 273. 10 S 1892.
68. [Review of] Catalogue of Canadian plants, Part VI.—Musci. John Macoun. Bull. Torrey Club 19: 275, 276. 10 S 1892.
69. [Review of] Fontinalacées—Monographie des. J. Cardot. Bull. Torrey Club 19: 317, 318. 10 O 1892.
70. [Review of] Enumeratio muscorum Caucasi. V. F. Brotherus. Bull. Torrey Club 19: 318. 10 O 1892.
71. Musci [of West Virginia]. Bull. W. Va. Agric. Exp. Sta. (no. 24) 2: 484–498. illust. "Je" [N] 1892.
    Also as a separate (under the title "West Virginia mosses"): Contr. Herb. Columbia Coll. no. 32.

1893

72. [Review of] Rabenhorst's Kryptogamen Flora, Part 21. Bull. Torrey Club 20: 260. 17 Je 1893.
73. The Jaeger moss herbarium. Bull. Torrey Club 20: 335, 336. 10 Au 1893.
74. Contributions to American bryology, III. Bull. Torrey Club 20: 393–405. 20 O 1893.
    Notes on the North American species of *Orthotrichum*.
    Also as a separate: Contr. Herb. Columbia Coll. no. 39 (paged 393–404, with lines rearranged throughout so as to bring all matter of original page 405 on page 404).
75. [Review of] Su alcune briofite fossili. U. Brizi. Bull. Torrey Club 20: 410. 20 O 1893.
76. Notes on two of Palisot de Beauvois species of *Orthotrichum*. Rev. Bryol. 20: 99. [D] 1893.

1894

77. Contributions to American bryology, IV. Bull. Torrey Club 21: 1–15. 25 Ja 1894.
    Notes on the North American species of *Orthotrichum*—II.
    Also as a separate: Contr. Herb. Columbia Coll. no. 44.
78. Contributions to American bryology, V. Bull. Torrey Club 21: 65–76. 20 F 1894.

Notes on the North American species of *Weissa* (*Ulota*).
Also as a separate: Contr. Herb. Columbia Coll. no. 48.

79. How to study the mosses. I. Observer 5: 82–86. Mr 1894.
80. Bryophyta [collected in southwestern Virginia]. Mem. Torrey Club 4: 172. 2 Ap; 173–188. 16 Ap; 189–191. 17 Ap 1894.
81. How to study the mosses. II. Observer 5: 114–120. illust. Ap 1894.
Polytrichum; Pogonatum.

82. Contributions to American bryology—VI. Bull. Torrey Club 21: 137–160. 25 Ap 1894.
I. Western species of *Orthotrichum* (137–159).—II Supplementary notes on the North American species of *Weissia* (*Ulota*) (159, 160).
Also as a separate: Contr. Herb. Columbia Coll. no. 52.

83. How to study the mosses. III. Observer 5: 151–157. illust. My 1894.
Catherinea; Georgia.

84. Contributions to American bryology.—VII. Bull. Torrey Club 21: 189–208. *pl. 197–203.* 25 My 1894.
A revision of the genus *Physcomitrium.* with descriptions of five new species.
Also as a separate: Contr. Herb. Columbia Coll. no. 54.

85. How to study the mosses, IV. Observer 5: 180–186. illust. Je 1894.
Funaria; Physcomitrium.

86. How to study the mosses, V. Observer 5: 215–219. illust. Jl 1894.
Ditrichum; Ceratodon.

87. How to study the mosses, VI. Observer 5: 246–251. illust. Au 1894.
Bryum; Mnium.

88. Contributions to American bryology.—VIII. Bull. Torrey Club 21: 343–372. *pl. 213–217.* 20 Au 1894.
A revision of the genus *Bruchia,* with descriptions of types, and one new species.
Also as a separate: Contr. Herb. Columbia Coll. no. 60.

89. How to study the mosses. VII. Observer 5: 306–311. illust. O 1894.
Leucobryum; Fissidens.

90. A revision of the genus *Physcomitrium.* [Abstract]. Proc. Am. Assoc. Adv. Sci. 42: 261. 1894.

1895

91. Contributions to American bryology.—IX. Bull. Torrey Club 22: 36–43. *pl. 227.* 15 Ja 1895.
A revision of the genus *Scouleria* with description of one new species.
Also as a separate: Contr. Herb. Columbia Coll. no. 69.

92. How to study the mosses. VIII. Observer 6: Pract. Micr. 17–21. illust. F 1895.
Dicranum; Bartramia.

93. Contributions to American bryology.—IX [X]. Bull. Torrey Club 22: 62–68. *pl. 229–231.* 26 F 1895.
1. The systematic position of *Physcomitrella patens* (62–65, *pl. 229, 230*).—2. On a hybrid growing with *Aphanorhegma serrata* Sull. (65–67. *pl. 231*).—3. On a European hybrid of *Physcomitrella patens* (67, 68).
Also as a separate: Contr. Herb. Columbia Coll. no. 72.

94. A revision of the genus *Scouleria.* [Abstract.] Proc. Am. Assoc. Adv. Sci. 43: 292. Mr 1895.
95. Some notes on the genus *Eucalypta* [*Encalypta*]. [Abstract.] Proc. Am. Assoc. Adv. Sci. 43: 292. Mr 1895.
96. A hybrid among the mosses. [Abstract.] Proc. Am. Assoc. Adv. Sci. 43: 292. Mr 1895.
97. Lycopodiaceae [collected in Bolivia by Miguel Bang]. Mem. Torrey Club 4: 271. 27 Ap 1895.
98. Filices [collected in Bolivia by Miguel Bang]. Mem. Torrey Club 4: 271–273. 27 Ap 1895.
99. Contribution[s] to American bryology.—XI. Bull. Torrey Club 22: 447–458. *pl. 248, 249.* 30 N 1895.
1. *Coscinodon Raui* and *Coscinodon Renauldi* (447–449 *pl. 248*).—2. *Dicranella heteromalla* and its varieties (449–452. *pl. 249*).—3. Notes on the genus *Leersia* Hedw. (452–458).
Also as a separate: Contr. Herb. Columbia Coll. no. 81.

1896

100. The luminous moss. [*Schistostega.*] Observer 7: 15–20. illust. Ja 1896.
101. [Review of] Die Laubmoose. Part 27, Hypnaceae. Bull. Torrey Club 23: 61, 62. 29 F 1896.
102. The humpbacked elves. [*Buxbaumia* and *Webera.*] Observer 7: 105–113. illust. Mr 1896.
103. [Review of] Remarques sur la nomenclature bryologique. Bull. Torrey Club 23: 110–112. 29 Mr 1896.
104. [Cryptogamic botany.] Salutatory. Observer 7: 161–163. Ap 1896.
105. Notices about specimens. Observer 7: 163. Ap 1896.
106. Vienna Exchange Office for Cryptograms. Observer 7: 163. Ap 1896.
107. The trailing Christmas-green. *Lycopodium complanatum.* Observer 7: 164, 165. *pl.* Ap 1896.
108. How I found *Schizaea pusilla.* Linn. Fern Bull. 4: 17–19. Ap 1896.
109. Vienna Exchange Office for Cryptograms. Bull. Torrey Club 23: 152. 30 Ap 1896.
110. [Review of] Musci Americae septentrionali exsiccati. Bull. Torrey Club 23: 159, 160. 30 Ap 1896.
111. The Brownies. [*Phascum* and *Pleuridium*]. Observer 7: 246–254. illust. My 1896.
112. Notes on the mosses. Observer 7: 255–257. My 1896.
113. Criticisms on Renauld and Cardot Musci Americae septentrionalis exsiccati. Bull. Herb. Boiss. 4: 476–478. Je 1896.
    Also as a separate.
114. The water nymphs. [*Fontinalis* and *Dichelyma.*] Observer 7: 442–447. illust. Jl 1896.
115. Criticisms of "New or less known species of acrocarpous mosses from North America and Europe" by N. C. Kindberg. Rev. Bryol. 23: 72, 73. [Au] 1896.
116. The umbrella mosses. [*Splachnum* and *Tetraplodon.*] Observer 7: 637–645. illust. O 1896.
117. Rediscovery of *Schizaea pusilla* in Newfoundland. Linn. Fern Bull. 4: 62, 63. O 1896.
118. An enumeration of the plants collected by H. H. Rusby, in Bolivia, 1885–1886.—II. Musci. Bull. Torrey Club 23: 471–499. 28 D 1896.
    Also as a separate, with double pagination, 471–499, and 9–28, 28a–28i; included in: Contr. Herb. Columbia Coll. no. 6.

1897

119. Emily L. Gregory. Bull. Torrey Club 24: 221–228. portr. 29 My 1897.
120. The sword moss. [*Bryoxiphium*] Pl. World 1: 1–5. illust. O 1897.
121. A revision of the North American species of *Ophioglossum.* Bull. Torrey Club 24: 545–559. *pl. 318, 319.* 30 D 1897.
    Also as a separate: Contr. Dep. Bot. Columbia Univ. no. 137.

1898

122. Four new species of *Ophioglossum.* Fern Bull. 6: 1, 2. Ja 1898.
123. The adder's tongue ferns. Pl. World 1: 85–89. *pl. 3.* Mr 1898.
124. List of mosses collected at Arlington, Staten Island, Sept. 27, 1896. Proc. Nat. Sci. Assoc. Staten Isl. 6: 54. Mr 1898.
125. *Anacamptodon splachnoides* (Frölich) Brid. Fern Bull. 6: 41, 42. Ap 1898.
126. A hybrid moss. Pl. World 1: 138. Je 1898.
127. Mosses of northern India. Bull. Torrey Club 25: 398. 15 Jl 1898.
128. [*Asparagus.*] Pl. World 1: 176. Au 1898.
129. Edible fungi. Pl. World 2: 9–11. O 1898.
130. Microscopic preparations of mosses. Fern Bull. 6: 89, 90. O 1898.

1899

131. A new Tertiary fossil moss. Bull. Torrey Club 26: 79–81. 8 F 1899.
    Also as a separate.
132. Fossil mosses. Pl. World 2: 108, 109. Ap 1899.
133. Variation in *Polypodium vulgare.* Fern Bull. 7: 34, 35. Ap 1899.
134. A bryological memorial meeting at Columbus, Ohio. Fern Bull. 7: 77, 78. Jl 1899.
135. A new *Grimmia* from Mt. Washington. Rhodora 1: 148, 149. *pl. 7.* 1 Au 1899.

1900

136. Distribution of the eastern species of *Mnium*. Bryologist 3: 4–6. Ja 1900.
137. (With Robert Statham Williams.) A new species of *Mnium* from Idaho and Montana. Bryologist 3: 6, 7. Ja 1900.
138. Mosses in February. Jour. N. Y. Bot. Gard. 1: 26–29. *f.* 6. F 1900.
139. Mosses in March. Jour. N. Y. Bot. Gard. 1: 40–43. *f. 9, 10*. Mr 1900.
140. How to know some of the commoner bryums. Bryologist 3: 16–19. illust. Ap 1900.
141. Mosses in April. Jour. N. Y. Bot. Gard. 1: 56, 57. *f. 13*. Ap 1900.
142. An ice storm. Jour. N. Y. Bot. Gard. 1: 72–74. *f. 16*. My 1900.
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157. The storing of seeds by squirrels. Torreya 1: 108, 109. 28 S 1901.
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180. The relations of plants to birds and insects. Pl. World **7**: 69, 70. Mr 1904.
181. Extremes meet. Pl. World **7**: 97–99. Ap 1904.
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190. Notes on nomenclature. V. Bryologist **8**: 49. 1 My 1905.
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The development of the shoot, male flower and seedling of Batis maritima L.[1]

DUNCAN S. JOHNSON

(WITH PLATES 1–3)

INTRODUCTION

The general structure of the vegetative organs, flowers and seeds of *Batis* have been studied more or less carefully by a number of workers and its possible relationship has been discussed by many more. Several quite different hypotheses have been published of the affinities of *Batis* with other Dicotyledons. These have been summarized in some detail, among others by Torrey (1853, p. 3), by Dammer (1893, p. 118), and most recently by Uphof (1930, pp. 355–367). I may here mention a few of the affinities that have been assigned to this plant, merely to show how unsettled the question of its natural relationship still is.

Patrick Browne (1756, p. 356) gave this plant its generic name and the first description that could adequately serve as a basis for guessing at its relationship. Kunth (1816, p. 193) places *Batis* among the Chenopodiaceae. Sprengel (1826, p. 901) thinks *Batis* may belong among the Coniferae. Seubert (1844, p. 753) compared the male spike of *Batis* with that of *Sarcobatus* and that of certain Chenopodiaceae and suggests that *Batis* resembles such Chenopodiaceous genera as *Salicornia*.

A. de Candolle (1873, p. 34) put the Batidaceae between the "Salsolaceae" and the Lennoaceae. Bentham and Hooker (1830, p. 88) rank the Batidaceae between the Phytolaccaceae and the Polygonaceae. Van Tieghem (1884) says that the affinities of the Batidales are quite obscure, but that *Batis* resembles the Chenopodiaceae in its male flower, the Phytoloecaceae in its pluricarpellous pistil and the Gyrostemonaceae in its dioecism. Baillon (1888, p. 254) places the Batidaceae between the Salicaceae and the Podostemonaceae. Dammer (1893, p. 118) after characterizing the genus by certain vegetative, anatomical and floral features, concludes that all evidence then available indicates that *Batis* is quite isolated from other dicotyledons. He places this order between the Amarantaceae and the Phytolaccaceae. Van Tieghem (1903, p. 363) places the Batidaceae in the "alliance" Piperales, between the Salicaceae and the "Liquidambaracees." Engler and Gilg (1924) put the order Batidales between the Juglandales and Fagales with the comment "steht vollig isoliert." Uphof (1930, pp. 355–367) gives an extended summary of the views of all earlier workers on the affinities of *Batis* and a good account

[1] Botanical Contribution No. 123 from the Johns Hopkins University.

of the habit, ecology and organography, both vegetative and reproductive, but he offers no opinion of his own regarding its affinities.

The present study of this fleshy-leafed salt marsh shrub of neotropical strands was made in order to determine what light the development and anatomy of the shoot, flowers and fruit of *Batis* may throw on the precise relationship of this genus. One still more general question in mind was that of the supposed primitiveness of this genus among dicotyledons.

MATERIAL

Male and female inflorescences and mature fruits of *Batis* were collected by the writer near Kingston, Jamaica, in July of 1919, of 1926 and of 1932. These were fixed in chrom-acetic acid fixative or in one of formol, acetic acid and alcohol. Ripe seeds from Jamaica were germinated in Baltimore in November 1926. Other material of this species has been collected for the author by Dr. John K. Small at Miami, Florida, by Dr. Louis J. Pessin in Louisiana and by Prof. J. C. Th. Uphof on the east coast of Florida. The seedlings grew for nearly two years in Baltimore. Transplanted mature plants lived a year and more but never flowered, even though watered with brackish water.[2]

Batis maritima L. is a maritime shrub or half shrub of wide distribution on both Atlantic and Pacific tropical coasts of the three Americas and of the Hawaiian Islands. It is a half-erect half-creeping plant with drooping branchlets (fig. 1). It has opposite, stipulate, half-cylindrical, fleshy leaves and inconspicuous individual flowers in compact spikes (or catkins). The fruits are compound, fleshy and persistently green. In external form the fruits resemble a diminutive potato tuber or the fruit of *Opuntia leptocaulis* (figs. 1, 2). Near Ferry River, west of Kingston, Jamaica and at other points *Batis* forms dense tangles, with its slender sprawling branches covering many square meters of low ground subject to tidal overflow by salt or brackish water. The plants here grow to about half a meter in height and are often overtopped, sometimes shaded out, by the black mangrove *Avicennia nitida* and by the salt marsh fern *Acrostichum aureum*. The rather extensive root system of mature *Batis* plants is made up chiefly of adventive roots arising on the creeping stems. These roots differ widely in size and in complexity of internal structure.

The often upright main stem or trunk of *Batis* may become three or four centimeters in diameter. It branches repeatedly near the ground and the slender, half-creeping branches arising from these main axes range

[2] Material was collected in Jamaica while studying other problems there, aided by a grant from the Bache Fund of the National Academy of Sciences.

three to eight or ten millimeters in diameter. From these half-erect branches are produced the green, 4-angled, erect and then drooping branchlets (or spurs) that bear most of the leaves and flowers (figs. 1, 3). The young stems have small, widely spaced vascular strands (see Solereder 1908, pp. 668, 1032), and Van Tieghem (1903, p. 363). The tracheal elements of these are chiefly spiral in type (figs. 15, 16). Leaf gaps and branch gaps are prominent in cross sections of the stem (figs. 8, 9, 10).

The leaves of *Batis* are opposite, glaucous and quite fleshy. When mature they are almost cylindrical in the upper third, while the middle is semicylindrical (fig. 14) and the basal fifth is decidedly grooved on the upper or adaxial side where it partially clasps about the stem (figs. 10, 11, 13, 19). The tip of the leaf is definitely pointed, sometimes really mucronate (figs. 2, 7, 16). The leaf is sessile and is united to the stem by a relatively small area of attachment at about half a millimeter above its clasping lower extremity (figs. 1, 5, 7, 19). Two leaf traces pass into each leaf (figs. 9, 20) but each immediately breaks up into two on entering the leaf. Just beyond the base the two median, and thus adjacent ones, of the four branches so formed unite to form a large median vascular bundle (figs. 7, 11, 13, 14). Later the marginal branch of each of the two original leaf traces forks once or twice further to give rise to the two or three branches that run upward in each half of the leaf (figs. 12, 13). Connected with the ends of many of the branchlets of the bundles of the leaf, are numerous small, isodimensional groups of short, scalariform tracheids (figs. 14, 16). These groups are most abundant near the tip of the leaf and most of them are nearer the dorsal or abaxial side. The tracheids differ strikingly from the (ordinary) xylem conducting elements of the leaf in having strongly reticulate thickenings instead of the spiral, or more rarely annular, thickenings characteristic of the vessels (figs. 16, 26). These reticulate tracheids are connected to the ends of the smaller vascular branchlets of the leaf. They seem to have no connection with any external opening, or water pore, nor with air spaces among the palisade cells. The function of these tracheids is perhaps, though this has not been demonstrated, the distribution of water from vascular bundles to the water storage tissue of the fleshy leaf (figs. 14, 15, 16).

The stipules: All descriptions of *Batis* found by the writer characterize its leaves as being without stipules. (See Patrick Browne, 1756, p. 356; Carl Linnaeus 1763, p. 1451; Jacquin 1763, p. 261; Swartz 1781, p. 373; John Lindley 1845, p. 386; Torrey 1853, p. 5; Dammer 1893, p. 119) This supposed lack of stipules has of course played a definite part in determining where the Batidales should be placed among the orders of the Dicotyledoneae.

In the present study, where paraffin sections of the buds and flowers were used, it became evident at once that stipules are constantly present on leaves from very young rudiments up to mature leaves, 6 or 8 nodes back from the terminal bud (figs. 9, 10, 12). The reason that they have not been noticed by earlier observers is the fact that they are very small, are soon covered by the leaf bases and that they often wither and drop off shortly after the leaves have fully matured. Then too most descriptions of *Batis* have been made from herbarium specimens, the stipules of which have withered and fallen in the pressing. In living plants the stipules are occasionally present on the fourteenth exposed node below the terminal bud.

The position of these stipules of *Batis* and their relation to the leaf itself correspond precisely with those given by Goebel (1923, p. 1422), i.e., they arise right and left from the leaf base just as leaflets or leaf teeth arise from the upper part of the leaf. This is evident in a view of the edges of the unopened leaves of a bud (figs. 10, 12, 19). Stipules can often be clearly seen also at each side of a leaf scar after the fall of the leaf, five or six internodes below the last attached leaf (fig. 20 below). Finally the position of the stipule and its intimate connection with the base of the leaf can be demonstrated indubitably in both longitudinal and transverse sections of the buds of *Batis* (figs. 9, 10). Stipules are also present on the bracts of both the male and the female spikes as will be described later.

The stipule as seen from the adaxial or abaxial side is a somewhat ovate, blunt-tipped structure with short, broad stalk (fig. 24). In transverse section the broader part of the stipule shows its thickness to be about half its width (figs. 9, 10). Stipules average 22μ in length, 20μ in width and their greatest thickness is about 10μ. The stalk is often thinner as well as somewhat narrower than the body of the stipule, and is also simpler in internal structure (figs. 10, 22). The internal structure of the stipule is little specialized. There is no vascular bundle. The surface cells of the body of the stipule are decidedly elongated radially, have bulging outer ends and contain moderate-sized nuclei but often have relatively large vacuoles (figs. 22, 23).

The possible function of the stipules is not yet determined. The small size of the stipules in proportion to the neighboring leaf rudiments makes it improbable that they can be of great importance in protecting the leaf rudiments within them. It is conceivable that the stipules have a glandular function, though no very definite evidence of this was obtained. The brownish amorphous substance found between the young leaves in cross sections of the bud may be a secretion of the stipules (fig. 23). This substance, which is soluble in hot water like a mucilage but whose source and chemical

composition is still unknown, may perhaps serve as a lubricant that protects the young leaf and flower rudiments.

THE MALE INFLORESCENCE AND FLOWER

All plants of *Batis* studied seemed strictly dioecious. The writer saw no cases, such as are referred to by Dammer (1893, p. 118), of plants bearing both staminate and pistillate flowers. Not even rudimentary flowers of the opposite sex have been found on plants bearing functional male flowers or those bearing functional female ones. Nor have rudimentary carpels (mentioned by Dammer p. 118) been seen in male flowers.

The male flowers of this species arise in solitary, axillary, four-cornered spikes. Each spike is composed of from ten to thirty pairs of decussate bracts. The six to ten pairs of broad, thick, concave bracts in the middle of the spike are fertile, i.e. each subtends a single staminate flower (figs. 4, 26, 35, 43, 47).

The structure of the mature male flower has been described and figured in considerable detail by Torrey (1853, Pl. XI, figs. 1–10). The bract subtending each flower is nearly circular, short-stalked and blunt-pointed (fig. 25). It is not merely concave upward but it has a decidedly thinner margin at the sides and above (figs. 25, 36, 43). The vascular strand that enters the petiole of the bract breaks up at the base of the blade into five main branches that radiate toward the margins of the blade and run nearer its ventral surface (figs. 25, 26). The three middle branches continue on two-thirds the way to the margin before forking again (fig. 25). Each of the two lateral branches soon forks (fig. 25). Then the twenty or more marginal branchlets of these five main bundles finally anastomose to form a complete vascular ring near the margin of the thickened central portion of the bract (fig. 25). From this marginal vascular ring a series of some twenty-five or thirty short branchlets run outward and dorsally each to end in a small group of water tracheids which lies nearer this dorsal or abaxial surface of the bract (figs. 25, 26, 28, 29). There are no vascular strands or water tracheids in the thin margin of the bract (figs. 25, 29). Each bract bears two small stipules at its base (figs. 12, 25, 42). It is evident from the above given description that the bract of the staminate spike is a decidedly more differentiated structure than is indicated by Torrey (1853, fig. 5).

Each staminate flower has four stamens alternating with four whitish, spatulate, slender-stalked, denticulate "appendages" or staminodia, called petals by Torrey, (figs. 26, 27, 31, 46). All eight of these structures in the quite young flower are enclosed in a sac-like perianth which finally forms a complete capsule which is flattened against the axis of the spike

and also against the under side of the next higher bract (figs. 26, 43, 47).

In the development of the male flower the perianth ("calyx" of Torrey 1853, p. 6) is the first structure to appear (figs. 35, 42). The upper, or adaxial, lobe of the perianth is the earliest part of it to appear, and is also the most rapid in growth. It thus soon bends over the top of the flower and then downward to completely cover the young stamens and staminodia (figs. 35, 36, 37). The ring-like perianth soon closes in from all sides and thus later leaves only a narrow, usually transverse, slit-like opening on the side next the subtending bract (figs. 29, 36, 39, 45). The lobes of the perianth sometimes abut when they meet (figs. 36, 38), but often one lobe overlaps the other, as is seen in either longitudinal or transverse section (figs. 39, 45). As the flower matures this slit becomes tightly closed and difficult to discover in either surface view or section. The perianth thus seems to form a practically completed capsule (figs. 26, 44, 47). The upper lobe of the perianth not only grows downward to cover the stamens, but its outer and middle portion grows outward and upward to form the so-called "crest" of the perianth. This crest finally protrudes between the projecting tip of the bract of its own flower and the thick, middle portion of the next bract above (figs. 26, 39, 47 above).

When the flower finally opens the stamens and staminodia push out of the perianth not by enlargement of the preexisting slit, where the lobes closed together during development, but through a *new* rift. This rupture is transverse to the perianth, on its outer side and is located well up toward the "crest" at its tip (fig. 47 below). This rift is clearly located in the upper of the two lobes of the perianth that were seen in the young flower, but it is below the crest of the opened perianth and not above it as Torrey (1853, p. 6) described it. This leaves the crest itself on the upper "lip" of the opened perianth and not on the lower one where Torrey locates it. Torrey evidently refers to the "lips" that are left above and below the rupture of the opened perianth (1853, p. 6). He says "The calyx is a little cup, consisting of two sepals, which are anterior and posterior to the axis and are united below the middle. The cup is compressed and somewhat two-lipped; the lower lip slightly cucullate and cristate transversely just below the margin" (see Torrey, 1853, fig. 4). Dammer (1893, pp. 118–119) says the perianth (Blütenhülle) is cup-like, closed at first then opening by a transverse rupture leaving the posterior lobe usually larger than the anterior (see Dammer, fig. 71 C. D). Neither of these accounts gives the development of the perianth and therefore they could not relate the line of rupture to the original opening in the young perianth as this study does.

A transverse section of the male flower in its lower half shows the perianth as a flattened ring of tissue five to eight cells in thickness with three

small vascular bundles in its thicker, adaxial wall (figs. 44, 46). Still lower down only one bundle was seen, but higher up there are several branches of each of the three primary bundles. Some of the branches from the two lateral bundles run around to the abaxial side of the perianth (figs. 26, 46). In the thickened upper portion of the perianth, on the outer abaxial side are found a few small groups of the water tracheids that are more abundant in the leaf and in the floral bract (figs. 26, 39).

The whorl of four staminodia (the "petals" of Torrey) stands just within the perianth, two at the right and two at the left of the midplane of the flower, thus alternating with the stamens (figs. 43, 44, 46). Each staminodium has a rather long thin stalk and a broad rhombic-ovate, wavy-margined blade (figs. 27, 31). The stalk is but five or six cells thick and ten or twelve cells wide, it contains no vascular bundle and its outer cell walls are not thickened or appreciably cutinized (figs. 32, 34). The blade of the staminodium is six or eight times as wide as the stalk, i.e., forty or more cells wide, but only four or five cells thick (figs. 31, 33). The surface cells of the abaxial face of the blade have greatly thickened and apparently cutinized walls (fig. 33). This wall is often nearly as thick as the cell cavity itself. The function of these walls, in structures which are enclosed in the perianth till they are practically mature, is not easy to guess, unless they serve to support these papery staminodia after expansion. The stamens would seem to be in no need of such structures for their protection, since they are protected till just before their expansion by both the perianth and the close overlapping of the subtending bracts.

No evidence was found that these so-called staminodia ever were functional stamens. The entire lack of vascular bundles, even at the base of the stalk, and likewise the presence of the cutinized wall on the outer cells of the blade would seem to be evidence against their staminal nature rather than for it.

The stamens of *Batis* arise as four rounded knobs in a ring about the center of the male flower. Two of them stand in the median plane of the flower and the other pair on the diameter at right angles to this (figs. 40, 43, 44). When the young stamen has elongated to two or three times its diameter, the upper half swells to form the anther, a vascular strand appears in its filament, and then four archesporial groups of cells appear in the anther (figs. 44, 46). The stamen matures into one of a usual angiosperm type, with 2-celled (4-sporangiate) introrse anthers (figs. 27, 46). Each anther is attached by its middle to the tip of the filament (fig. 27). The wall of the anther is four cells thick and the hypodermal (parietal) layer is the chief mechanical layer of the wall. The thickened strips on the radial walls of these cells are unusual in that they may be diagonal or

even transverse instead of being always radial as in most angiosperms (figs. 48, 50). The tapetal layer is of darkly staining and rather constantly binucleate cells (fig. 48). The diameter of each tapetal nucleus is about half that of the microspore nucleus (fig. 48).

The microspores of *Batis* are minute (16 to 18μ in diameter) spherical and smooth walled, except for four outward distentions of the thin inner wall which apparently serve as the sprouting points of the microspore (figs. 48, 51). The most mature microspores seen in the anther were binucleate, but the two nuclei could not be shown to be separated by a wall (fig. 51). No microspores were found germinating on the stigma but it is assumed that the somewhat smaller nucleus nearer the wall of the spore is the generative nucleus.

It is hoped that studies, already initiated, on the development of the female inflorescence and seed of *Batis* will be completed in a year. The report of that study will include a discussion of the theoretical bearings of its results and likewise of the phylogenetic implications of the facts recorded in the present paper.

GERMINATION

No record has been found of any observations of the germination of the seeds of *Batis* and no very young seedlings were found in any of the several habitats where the plant was collected in Jamaica. The perfectly healthy appearance of the well stored embryos in the seeds led me to attempt germination in Baltimore, in October 1926, of seeds brought from Jamaica in August of that year. Seeds planted in potting soil mixed with an equal part of sand germinated promptly, (fig. 5) and, watered at first with brackish water later fresh water only, grew quite rapidly for the first four months (figs. 5, 5a, 6) and then slowed down till after reaching a height of 25 to 30 centimeters in 1928 they gradually lost their leaves and died down in the spring of 1929.

As the seed, when mature, has no endosperm or perisperm the mechanics of germination is externally relatively simple. The fact that the radicle of the embryo points toward the axis of the spike makes it necessary that in its exit the root of each seedling should not only burst the tough endocarp of its own seed case, but should also push apart the other seed cases of its own ovary and likewise those of its mate on the other side of the spike.

The cotyledons of the young seedling are fleshy from the time they open (fig. 5). The paired secondary leaves which follow the cotyledons in rapid succession are also thick and succulent even before their opening from the bud (fig. 5 at left). The primary root branches early (fig. 5a) but

the primary axis of the stem under greenhouse conditions remains simple until 10 centimeters or more in height. (fig. 6). The oldest plants grown had but few, short and weak lateral branches.

The attempt to grow in the Botanical Garden at Johns Hopkins University mature rooted plants collected on the shore of the Gulf of Mexico in November 1932 succeeded until spring when the plants were moved from the greenhouse to the open. Then the rabbits, which seemed to enjoy the salty shoots of *Batis*, ate the tips off nearly all the plants. When plants from Florida were planted in a sandy soil with wet subsoil in February 1934 and protected from the rabbits the shoots grew in four months to 45 centimeters in height. None of these shoots had flowered, however, up to June 15, 1934. It is clear that the time required for the seedling to mature and flower can be most satisfactorily determined from seedlings growing in their native habitat.

SUMMARY

This study was undertaken to determine the course of development of the shoot, flower and seedling of *Batis* and the evidence these offer concerning the relative primitiveness and probable relationship of this apparently isolated genus. The succulent shoots of this plant bear fleshy, sessile leaves, attached above a median basal lobe. Each vascular branchlet of the leaf usually ends in a small group of water tracheids lying just beneath the four- or five-tiered palisade layer of the leaf. These tracheids have reticulate thickenings instead of the ring-like or spiral ones that characterize the conducting elements of the xylem. Each leaf bears a pair of quite diminutive, early-withering stipules concealed by its clasping base. These stipules are perhaps glandular in function. The withered stipules often adhere to the stem for several nodes below the oldest attached leaf.

The solitary, axillary, staminate spikes consist of from ten to thirty pairs of broad, thin-margined bracts, of which each bears a male flower in its axil, except one or two pairs at the base and a couple of pairs at the tip. Each bract has two small stipules at its base and each is furnished with numerous vascular strands and water tracheids, both confined to the thickened middle portion. Each male flower consists of four stamens, with two-celled anthers and four broad-bladed papery staminodia outside the whorl of stamens. Not even rudiments of carpels were seen. Stamens and staminodia are enclosed by a sac-like, crested perianth that starts as a ring, closes in to a very small slit and then finally opens by a new rift, far above this original opening of the perianth, but below the crest.

Seeds of *Batis* germinate readily in the greenhouse. Seedlings have

fleshy cotyledons and leaves from the start. The root branches early but the erect stem remains unbranched until 12 or 15 centimeters in height. No seedlings or older plants transplanted from Florida or Louisiana have yet developed flowers in the greenhouse.

No essentially primitive structures have been discovered in this study. The perianth itself seems a decidedly specialized one.

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Explanation of plates

Abbreviations: A, apex of stem, leaf or spike; ax. b, axillary bud; B, base; br, bract; cr, crest of perianth; fl, flower; lf, leaf; lg, leaf gap; lt, leaf trace; pe, perianth; pt, petiole (short leaf stalk); S, stem, sd, staminodium; sn, stamen; sp, spike; st, stipule; wt, water tracheid.

Plate 1

Fig. 1. Living branch of a pistillate plant, showing drooping branchlets, leaves, half-grown and matured fruits. $\times\frac{3}{4}$.

Fig. 2. Several mature, living, green, compound fruits, showing persistent stigmas. $\times 1\frac{1}{2}$.

Fig. 3. Branch of staminate plant (alcoholic) showing size and form of male spike. $\times 1$.

Fig. 4. Several male spikes showing separated bracts and burst perianths near tip of spikes at left and in middle; extended stamen on each side of vertical spike at right and of horizontal spike at left in middle. $\times 1\frac{1}{2}$.

Fig. 5. Group of seedlings three weeks from sowing at Baltimore, showing cotyledons, epicotyl and first cauline leaves. $\times 1\frac{3}{4}$.

Fig. 5A. Seedling of three weeks showing branching of root. $\times 1$.

Fig. 6. Seedlings four months from sowing showing stem, fleshy leaves and scars of earlier, deciduous, cauline leaves. $\times 1$.

Plate 2

Fig. 7. Longitudinal section of a stem apex bearing leaves, axillary buds and a male spike at left. $\times 10$.

Fig. 8. Transverse section of internode of half-year old stem showing arrangement of vascular bundles of the stem including the leaf traces and large leaf gaps. $\times 10$.

Fig. 9. Transverse section through the sixth node below the bud of a 3-month shoot showing leaf bases, stipules, leaf traces, leaf gaps and vascular system of stem after establishment of a complete cambium ring. $\times 11$.

Fig. 10. Transverse section just below a young node showing clasping leaf bases and the hidden stipules. $\times 11$.

Fig. 11. Transverse section of stem apex (at center) with five pairs of leaves showing arrangement of these and of the vascular bundles in each leaf. $\times 27$.

Fig. 12. Transverse section of male spike showing stem, leaves, a young flower and six stipules. $\times 30$.

Fig. 13. Transverse section of young leaf near base showing vascular strands and epidermis differentiated. $\times 27$.

Fig. 14. Hand section across living mature leaf showing shape of leaf in upper half, three main vascular bundles, many branchlet bundles, and groups of water tracheids beneath the palisade layer. $\times 11$.

Fig. 15. Detail of cross section of living leaf showing palisade cells with chloroplasts, vascular bundle endings and air spaces beneath a stoma. $\times 100$.

Fig. 16. Longitudinal section of tip of young leaf showing vascular bundle ending in group of water tracheids. $\times 127$.

Fig. 17. Epidermis of living leaf showing shape of epidermal cells and varied position, size and form of guard cells, and striated outer walls of the subsidiary cells. Apical end of piece upward. $\times 100$.

Fig. 18. Adaxial face of basal end of living, mature leaf, cut off from stem, showing lobe below petiole and axillary bud and two stipules above the cut off petiole. $\times 7$.

Fig. 19. Tip of living branch showing bases of two leaves with their lower lobes (below at right and left of stem) the right stipule of left leaf and left stipule of right leaf between these leaves, and leaf scar and stipules of a torn off leaf across face of stem. $\times 25$.

Fig. 20. Scar of cut off leaf from eighth node below bud showing its stipules and leaf traces and the axillary bud lying against the surface of the *stem*. The radiating lines indicate the directions of cell rows running out from the depression of stem at base of leaf. $\times 77$.

Fig. 21. Axillary bud, leaf scar, leaf traces and stipules of leaf at node 14 below bud and node 6 below lowest (oldest) attached leaf. Stem and upper leaves living,

stipules brown and rather shrivelled. The two lateral leaves of the axillary bud are seen from the end. Large leaf in middle is the first on abaxial side of the bud. ×77.

Fig. 22. Longitudinal (approximately sagittal) section of three-fourths grown stipule showing internal structure. Part of stipule of the opposite leaf at top. ×295.

Fig. 23. Cross section of young stipule near middle showing internal structure. Also, at three corners of the stipule, the slime-like substance that fills interspaces between leaves and stem. ×295.

Fig. 24. Outer face of mature, brownish stipule from leaf 8 below bud on a living stem showing surface formed by ends of radiating cells. ×107.

Fig. 25. Ventral surface of bract subtending male flower (alcoholic) showing form, stalk, one of its stipules, plan of the vascular system with numerous terminal groups of water tracheids. ×25.

Fig. 26. Sagittal section of male flower and its bract showing closed perianth, two stamens and two staminodia, with water tracheids in both. ×25.

Fig. 27. A ripe stamen with adjoining staminodium, showing insertion of anther and form of staminodium. ×11.

Plate 3

Fig. 28. Tangential section, near margin, of bract of male spike showing vascular bundle endings and groups of water tracheids. ×150.

Fig. 29. Tangential section of a bract and perianth of a male flower showing water tracheids of bract, the nearly closed transverse slit of the young perianth and, near center, part of a second bract. ×25.

Fig. 30. Detail of margin of slit in a nearly closed perianth. ×150.

Fig. 31. Surface view of right half of blade of a staminodium showing wavy margin and cell arrangement. ×55.

Fig. 32. Longitudinal section of base of stalk of a staminodium showing lack of vascular bundles and of cutinized epidermis here. ×150.

Fig. 33. Part of longitudinal section of blade of staminodium showing very thick cuticle on outer side. ×150.

Fig. 34. Transverse section of stalk of staminodium showing simple structure and complete lack of vascular tissue. ×150.

Fig. 35. Longitudinal section of tip of male inflorescence showing three young flowers below with their subtending bracts and two very young ones just below apex. ×50.

Fig. 36. Sagittal section of male flower and bracts showing perianth still open and very young stamens and staminodia. ×50.

Fig. 37. Sagittal section of flower shown in last figure, but two sections beyond, showing nothing of slit in perianth. ×50.

Fig. 38. Sagittal section of somewhat older male flower showing perianth crested but slit still open. ×25.

Fig. 39. Sagittal section of older male flower showing crest well developed and upper lobe of perianth widely overlapping lower. ×25.

Fig. 40. Similar section of practically mature flower showing crest and long bent-over blade of staminodium. ×25.

Fig. 41. Longitudinal section of two anthers of young flower. ×250.

Fig. 42. Transverse section of young male spike showing stem at left, leaf sub-

tending whole spike at right and four flowers with their perianths and subtending bracts. ×20.

Fig. 43. Nearly transverse section of older spike showing in each of two upper flowers, positions of the four stamens and four staminodia. ×25.

Fig. 44. Cross section of half-grown male flower showing structure of perianth, staminodia and anthers. ×150.

Fig. 45. Somewhat obliquely transverse section of a staminodium and of overlapping lips of perianth. ×150.

Fig. 46. Nearly transverse section of single mature male flower showing distribution of vascular bundles in perianth, the staminodia and nearly mature anthers. ×27.

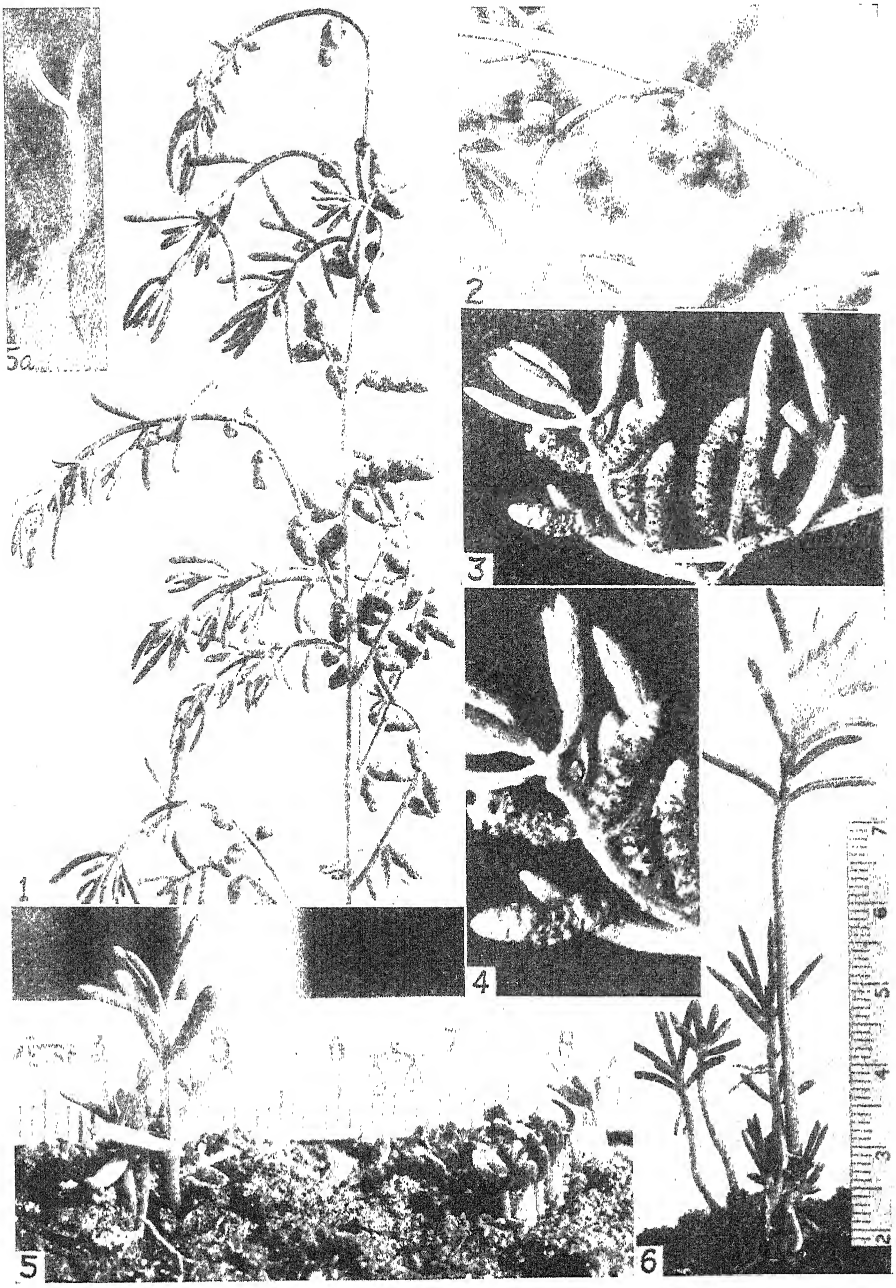
Fig. 47. Longitudinal section (diagonal) of mature (but unusually short) male spike showing sagittal sections of two unopened flowers and (below) two flowers in which stamens have burst through perianth, leaving "crest" of latter above the rupture. ×7.

Fig. 48. Part of longitudinal section of wall of anther showing also spore mother cells and binucleate tapetal cells. ×250.

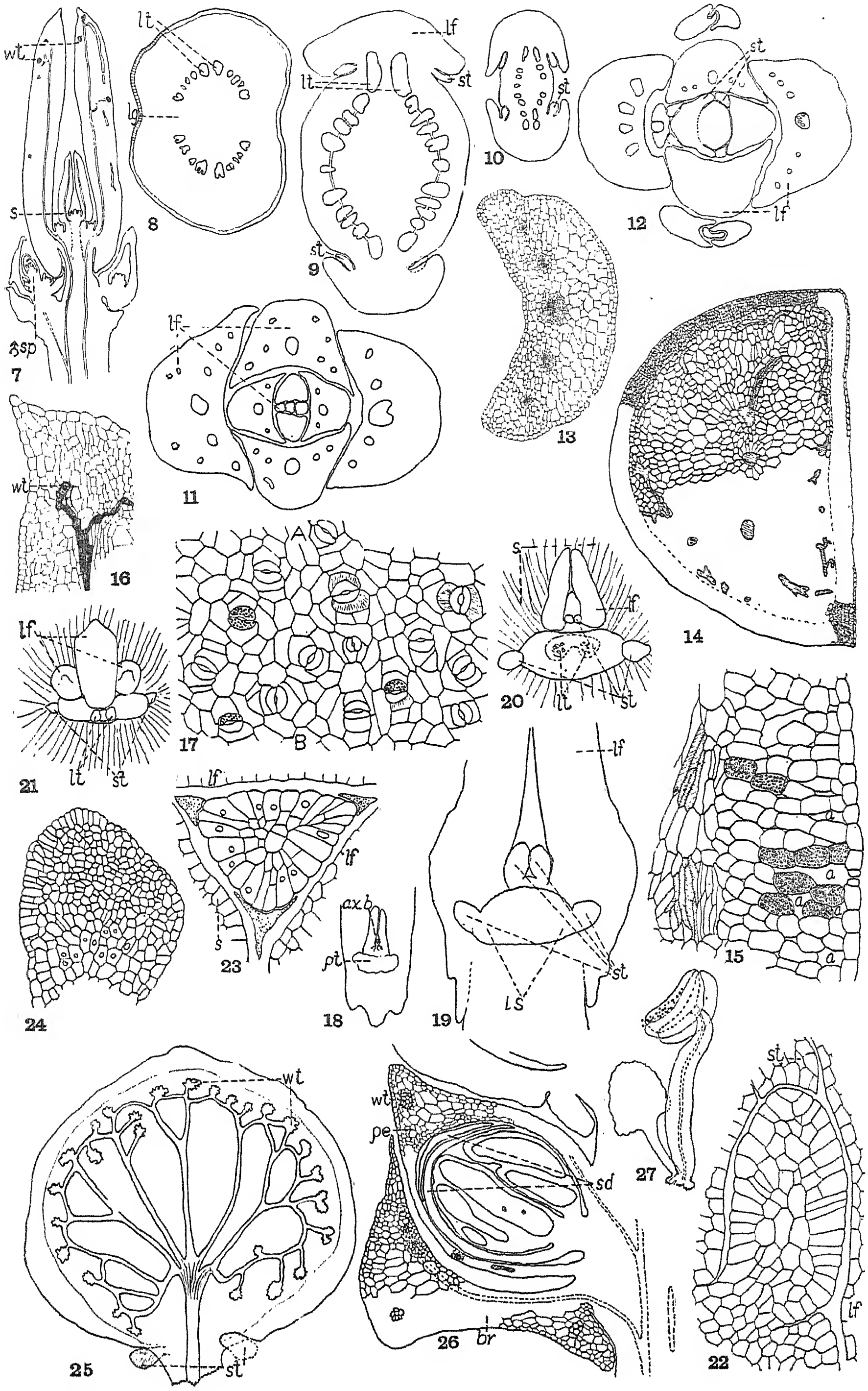
Fig. 49. Single uninucleate microspore. ×290.

Fig. 50. Part of cross section of wall of mature anther showing mechanical layer and nearly ripe binucleate microspores. ×250.

Fig. 51. A ripe binucleate microspore showing thickened wall and four germ pores. ×800.



JOHNSON: BATIS MARITIMA



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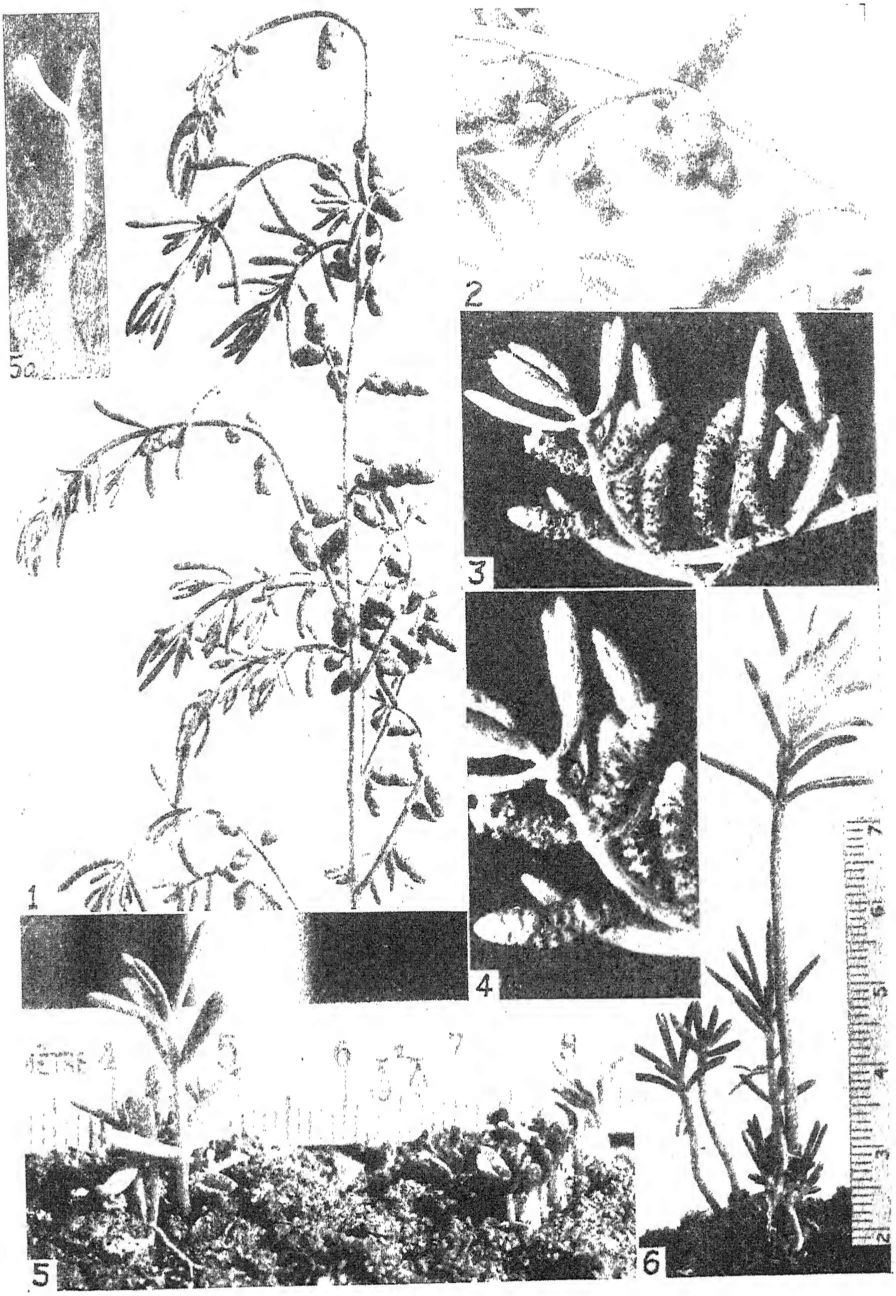

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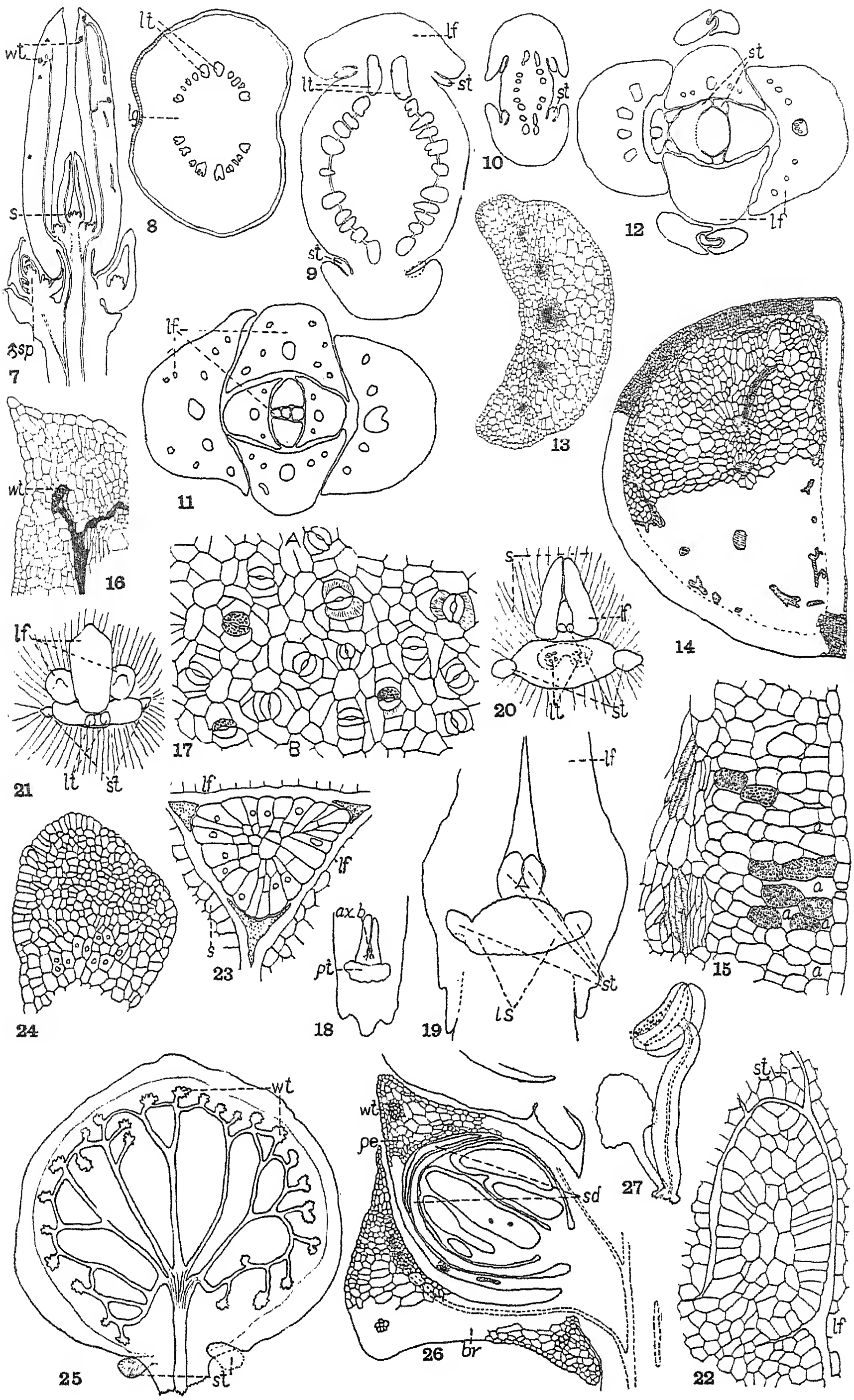

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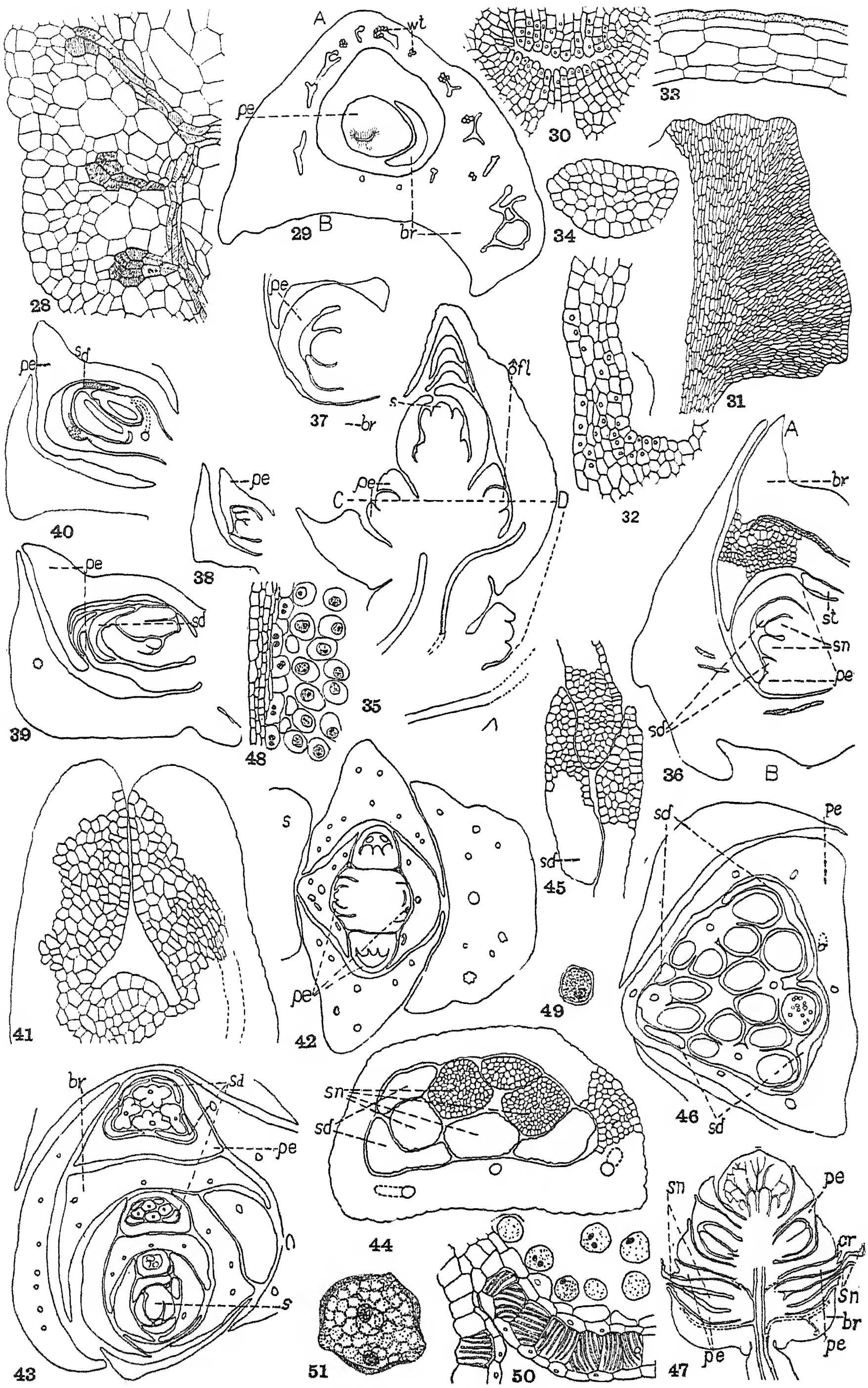


JOHNSON: BATIS MARITIMA

Riccia fluitans L.—a composite species

Annetta M. Carter

(with plates 4 and 5)

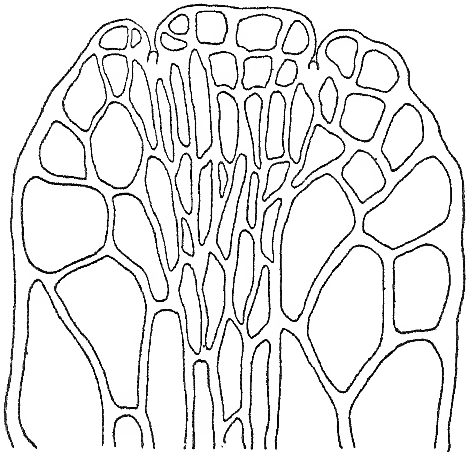
A survey of the literature on *Riccia fluitans* L., commonly thought of as an aquatic liverwort, shows that the species has been an object of controversy for some time. There is still some doubt in the minds of investigators as to the exact status of *Riccia fluitans* L. Some believe it to be a composite consisting of the aquatic forms of several terrestrial species of Riccia, while others still believe in treating it in the conventional way, as a distinct species which has both aquatic and terrestrial forms.

In confirmation of the conception of *Riccia fluitans* L. as a composite species, there is Von Gaisberg's (1921) work in Goebel's laboratory at Munich. He carried on cultural experiments with aquatic material from two different localities, from the university greenhouse at Munich, and from the vicinity of Starnberg in Bavaria, and with both he obtained similar results. That is, material from each of these localities, when grown on soil, developed into a sterile "broad form." The interesting point here is that Familler had classified the material from near Starnberg, presumably on its morphological characters, as *Riccia Huebeneriana* Lindenberg. Cross sections of the broad material showed that the outer portion of each flank of a thallus contained a single large air chamber, but that elsewhere the chambers appeared to be in two layers and sometimes, in the median portion, in three layers. According to Evans (1922), these characters might be sufficient to distinguish the broad material from *Riccia Huebeneriana* Lindenberg (as it is usually described) but they are not sufficient to separate it from the "forma *canaliculata*" of *R. fluitans* L. Donaghy (1916), after a series of observations on *Riccia fluitans* as it occurs in Indiana, came to the conclusion that the sterile terrestrial plants derived from aquatic plants were distinct from the so-called terrestrial form which is fertile. He also noted a slight widening in the apices of the aquatic thalli after they had come into contact with the soil. Familler (1920) is firm in the opinion that *Riccia fluitans* L. "consists of two or three aquatic forms of various Ricciae." There is no cultural proof, however, that his characters are not variable.

During the past three years, observations on California forms of *Riccia fluitans*, both in the field and under cultural conditions, have been made. The species was first reported (Evans, 1923) as growing in California by Mrs. E. C. Sutliffe of the California Academy of Sciences who collected it in Lily Lake, Marin County, in September 1921. The next known collection of *Riccia fluitans* in California was made by Herbert L. Mason in

October 1928 in the sloughs of the San Joaquin River, San Joaquin County. This extension in the distribution of the species has not previously been published.

The ecological conditions in the above two California localities where *Riccia fluitans* has been collected differ considerably. Lily Lake is a small pond shaded by redwoods, California bay laurels, and oaks. It is near the coast in the redwood fog belt; so the air temperature range is probably comparatively small. A November temperature of 44.2°F. was obtained. The aquatic thalli grow partially submerged among fallen tree trunks near the edge of the pond. They vary in breadth from 1 to 1.5 mm. The sloughs



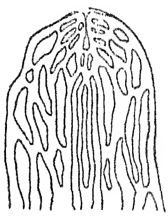


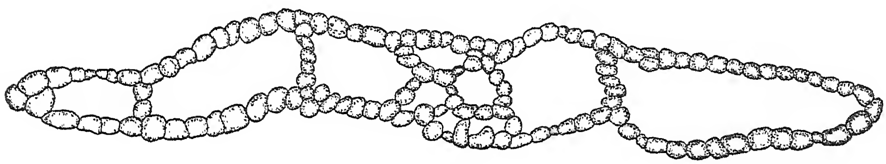
Fig. 1. Tip of a branch (with two growing points) from a broad thallus growing in small pot in the window box. Surface view showing the air chambers in outline. ×25

Fig. 2. Tip of a branch (with one growing point) from a narrow thallus growing in small pot in the window box. Surface view showing the air chambers in outline. ×25

near Holt, on the other hand, present an entirely different aspect. Here, the water is partially shaded by willows or by tules which grow out into it in the shallower areas that are not submerged throughout the year. For this locality a temperature range in the water of 39.6°F. was obtained, that is, 42.8°F. in December and 82.4°F. in July, and doubtless the temperature goes considerably above and below these two points. The aquatic plants float just under the surface of the water, either among the tules or in more open, deeper water in the shade of the willows, while a few terrestrial plants are found growing on floating logs or on the steep, moist banks above the surface of the water. All of the aquatic thalli are narrower than those from Lily Lake, few being more than 0.5 millimeter to 0.75 millimeter broad. This difference in breadth between the *Riccia fluitans* L. from

Lily Lake and that from the Holt sloughs immediately raises the question as to whether the thalli of the plants from these two localities show constant morphological characters that are dissimilar.

Cultures, terrestrial and aquatic, of material from both of these California localities were grown in the laboratory and in the open court of the Life Sciences Building of the University of California. The Lily Lake material remained consistently of the broad type, but the aquatic Holt material, when planted on soil, developed into two distinct types of thalli, a broad type and a narrow type. Cross sections of the broad thalli from both localities show each flank to contain from one to three large air chambers in one story, while the central area contains small or medium-sized chambers



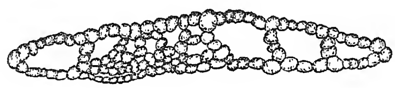


Fig. 3. Broad thallus from pot in the window box. Cross section, ×50.
Fig. 4. Broad thallus from Pot C in court. Cross section, ×50.

in two stories. The narrow thalli which developed from the Holt aquatic material, on the other hand, have a single small or medium-sized air chamber in each flank and small or medium-sized chambers, occasionally in two, but usually in three to four stories in the rest of the thallus. Surface views of the air chambers in the two types of thalli show that those in the broad thalli are polygonal while those in the narrow thalli are long and narrow both in the flanks and in the central region. In addition to the differences, between these two forms, in the type and arrangement of the air chambers, are the differences in growth form when on soil. The broad type of thallus is thin, has short, broad-angled dichotomies, and tends, when not crowded, to grow in "fan-shaped rosettes." The narrow thalli are slender and comparatively thick, have long, acute-angled dichotomies, and tend to spread out over the substratum rather than to form a definite rosette. Another point is that the narrow type of thallus is fertile (spores measure 75–94 microns in maximum diameter in plants grown in the laboratory, while those collected in the field, aquatic, were 84–108 microns

in maximum diameter), and the broad form, so far as the experiments carried through determine, is sterile.

Since cross sections of the two types of thalli showed such differences in the size and arrangement of the air chambers, it seemed as though each type should have a definite width-thickness ratio. A large number of sections were made of both wide and narrow thalli grown under various conditions. (The "submerged" thalli were those which had been returned to an aquatic habitat after having grown on soil for some time. When treated in this way, they became narrower, but their air chamber characteristics

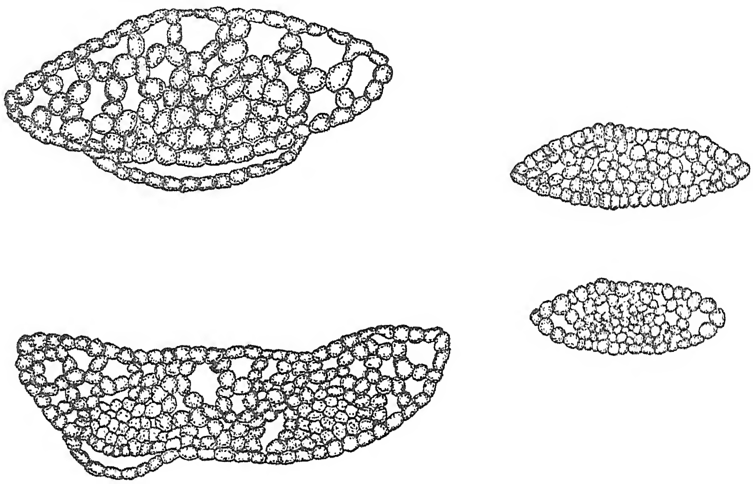


Fig. 5. Narrow thallus from small pot in window box. Cross section, ×50.

Fig. 6. Narrow thallus from small pot in window box. Cut near the apex behind two growing points. Cross section, ×50.

Fig. 7. "Submerged" narrow terrestrial thallus. Cross section, ×50. (Note that it differs from the other narrow thalli only in that it is more compact.)

Fig. 8. Narrow thallus from Pot C in court. Cross section, ×50.

remained constant.) At first, it seemed as if this width-thickness ratio could be used as a definite means of separating the two forms (tables 1, and 2) but further study showed that there was overlapping in a few instances.

In order to show that the broad and narrow terrestrial thalli developed from two distinct aquatic types of thalli, material was selected, on the basis of its air chamber characteristics, from a mixed aquatic culture collected at Holt. Sections were made of part of each thallus and the remainder of each thallus was planted on soil and placed in the window box. Those thalli that had an air chamber arrangement characteristic of the narrow type of thallus grew into narrow thalli on the soil, and those that had the wide type

of air chambers grew into wide thalli. After an interval of seven weeks sections were again made of portions of each thallus and the width-thickness ratio before and after being planted on the soil was compared (table 3.) As in the other width-thickness ratio comparisons there is slight overlapping here, but the results show quite definitely that the ratio for a given type of thallus is fairly constant for a given habitat. The *aquatic* narrow thalli have an average width-thickness ratio of 1.99:1 and the *terrestrial* narrow thalli, of 4.4:1; while the aquatic broad thalli have an average width thickness ratio of 2.91:1 and the terrestrial broad thalli, of 6.8:1. If both the width-thickness ratio and the air chamber characteristics are considered, there should be no difficulty in distinguishing the two types of thalli.

TABLE 1

Average of cross section comparisons

TYPE OF THALLUS	WIDTH	THICKNESS	RATIO
Narrow terrestrial thalli from Pots B and C and small pot in window box.	681.26	264.57	2.60
"Submerged" narrow terrestrial thalli.	449.00	160.00	2.76
Narrow terrestrial thalli collected at Holt, 7/29, 9/27, 1931.	677.60	191.90	3.53
Fruiting aquatic thalli collected at Holt, June 15, 1930. Narrow type.	444.12	199.37	2.28
Wide terrestrial thalli from Pots C and D and small pot in window box.	1406.16	199.08	7.07
"Submerged" wide terrestrial thalli.	658.35	120.21	5.48
Mixed aquatic thalli from Holt, July 29, and Sept. 27, 1931.	709.03	173.55	4.35
Aquatic thalli from Lily Lake, February 27, 1932. Broad type.	897.28	175.35	5.18

TABLE 2

Maximum—minimum measurements from cross section comparisons

TYPE OF THALLUS	WIDTH	THICKNESS	RATIO
Narrow terrestrial thalli from Pots B and C and small pot in window box.	800–396	352–110	3.77–2.11
"Submerged" narrow terrestrial thalli.	528–330	176–154	3.38–2.01
Narrow terrestrial thalli collected at Holt, September 27, 1931.	759–561	220–154	3.94–3.11
Fruiting aquatic thalli collected at Holt, June 15, 1930.	539–363	330–154	2.78–1.63
Wide terrestrial thalli from Pots C and D and small pot in window box.	1980–682	275–110	8.18–5.60
"Submerged" wide terrestrial thalli.	1045–462	154– 88	8.63–3.83
Mixed aquatic thalli from Holt, July 29, and Sept. 27, 1931.	1078–208	253–121	6.64–1.95
Aquatic thalli from Lily Lake, February 27, 1932.	1100–704	231–121	7.27–3.85

The fact that environmental conditions play an important part in determining the appearance and growth form of *Riccia fluitans* was demon-

TABLE 3

Comparison of broad and narrow thalli before and after planting on soil

	AQUATIC				TERRESTRIAL			
	NARROW THALLI							
	Thick.	*Width*	*Ratio*	*Aver.*	*Thick.*	*Width.*	*Ratio*	*Aver.*
	165	209	1.26		198	979	4.94	
I	209	330	1.57	1.607	209	825	3.94	4.38
	165	275	1.66		121	517	4.27	
	198	385						
II	154	187	1.21	(died)	—	—	—	
	176	286	1.62		220	847	3.85	
III	121	297	2.45	2.02	176	979	5.56	
	143	286	2.00		220	935	4.25	4.44
					253	1100	4.30	
					935	220		
IV	187	473	2.52	2.26				
	176	352	2.00					
	BROAD THALLI							
	165	594	3.6		220	1265	5.75	
	143	440	3.07		220	1320	6.00	
I	198	528	2.66	3.158	209	1254	6.00	6.08
	176	528	3.00		187	1232	6.58	
	143	495	3.46					
II	220	550	2.5	2.5	220	1595	7.25	
					220	2563	11.65	
					231	1496	6.47	7.37
					220	1155	5.25	
					176	1210	6.25	
	165	550	3.33		187	1100	5.88	
	176	506	2.87		220	1683	7.65	
	176	495	2.81		187	1243	6.64	
	165	429	2.60		176	1628	9.25	6.96
III	165	495	3.00	3.07	187	1375	7.35	
	143	550	3.84		220	1100	5.00	
	176	429	2.43					
	198	605	3.05					
	154	572	3.71					

The measurements are in microns.
The ratio is on the basis of the thickness of the thallus being 1.

strated in a series of observations made on the terrestrial cultures growing in the court. (These terrestrial cultures were in pots twelve inches deep

and fourteen inches in diameter. The pots were filled with soil to within five or six inches of the top and were partially submerged in the pool. Due to the depth of the cultures in the pots, the thalli on the south side were shaded during a large part of the day.) During the summer months, the gross aspect of the mass of thalli on the sunny side of the pots is decidedly purple, except in the central area where the conditions, although sunny, are very moist. Closer observation, however, shows that it is the broad thalli, rather than the narrow ones, which develop the greatest amount of anthocyanin pigment. Formation of this pigment takes place rapidly. Two days after a thallus was transplanted from the shady side of the pot to the sunny side it was beginning to show pigment at the base of the thallus, and after five days it was a deep purple except at the very apex. In addition to the formation of the pigment in the thalli on the sunny side of the pot, there was a noticeable slowing up of the growth rate in these same thalli. As winter approached, the purple coloring began to disappear from the plants, and by the last week in November there was not the slightest evidence of anthocyanin pigment in any of the thalli. In the first week of the following March, after several bright, sunny days, the broad thalli were beginning to show the return of the pigment. Cross sections of the wide, purple thalli showed that the pigment was confined, for the most part, to the single, outer layer of cells. In all cases, it was much more dense in the cells of the dorsal surface and diminished gradually in the cells on either flank of the ventral surface. In a few cases, the pigment was found in the unistratose lamellae between the air chambers. The pigment seems to form first in the older parts of the thallus branches, and there is none at all noticeable right at the growing point. Although these observations on the formation of anthocyanin pigments in *Riccia fluitans* touch only upon the surface of the question, it seems to me that they show clearly that the purple coloring in this plant is due entirely to seasonal, environmental changes, and that therefore the presence of the pigment may not be safely used as a character for the classification of the species nor for the classification of any form of the species.

The question of nomenclature in the broad and narrow forms is a difficult one. The *Riccia fluitans* described by Linnaeus cannot be definitely determined without having access to the type material in order to study the arrangement of the air chambers, and there is no record of a type specimen of *Riccia fluitans* in the Linnean herbarium. Since the broad type of thallus is more abundant than the narrow type in the Holt material and since it seems to be the exclusive type in the Lily Lake material, one is inclined towards the belief that it (the more abundant aquatic form, at least in the California material) may represent the type. If this should prove to

be the case, the name *Riccia canaliculata* (Hoffmann) would be free for use on the narrow terrestrial material which corresponds very closely with the description of the above species given by Familler (1920). The broad material, on the other hand, corresponds closely with Familler's "*Riccia Huebenerana*" Lindenberg, except that the California material is consistently sterile. The fact, however, that the California material is sterile agrees with Von Gaisberg's (1921) observations on the "broad form" from Starnberg which Familler had identified as *Riccia Huebeneriana*. Both broad and narrow types grow well, either on land or in the water; so the distinction of one being primarily terrestrial does not hold with our California material. The fact that I have found so much variation in my broad material corresponds with Familler's observations on *Riccia Huebeneriana* and *R. pseudo-Frostii* Schiffner where he found that one could be transformed into the other quite readily. Evans (1923), however, states that in North America *Riccia pseudo-Frostii* Schiffner is replaced by *Riccia Sullivantii* Austin. Therefore the question of whether *Riccia Sullivantii* could be confused with the California broad form might be raised. Dr. Marshall A. Howe kindly provided some living material of *R. Sullivantii* from the New York Botanical Garden and it has been kept growing on soil in the window box. Comparisons of this material with both of the California forms, however, show it to be quite distinct—the central tissue is much better developed; the whole aspect of the cross sections, although the air chambers are in one to three stories, is different; and the median sulcus is much better developed than in any of the California material of these investigations.

Although there is still room for more work on *Riccia fluitans* and the closely related species, it seems to me that in this study of its morphology and behavior several of the important questions that have been raised concerning it are advanced towards settlement. The more important points brought out in this study of *Riccia fluitans* L. as it occurs in California are as follows:—

1. The aquatic material, as it occurs in the sloughs at Holt, seems uniform when observed macroscopically, but when planted on soil two types of thalli develop,—broad and narrow.

2. The broad thalli on soil cultures are characterized, externally, by being thin, having short, broad-angled dichotomies, and growing in "fan-shaped" rosettes. The air chambers tend to be polygonal, and a cross section of the thallus shows that the flanks are one-storied and that each flank contains from one to three large chambers, while the central area contains small, or medium-sized chambers in two, or occasionally, in three stories.

3. This broad material, in so far as can be determined by vegetative characters, seems to correspond closely to Familler's *Riccia Huebeneriana* Lindenberg.

4. The narrow thalli on soil cultures are slender and comparatively thick, have long, acute-angled dichotomies, and tend to spread out over the substratum rather than to form a definite rosette. A surface view of the thalli shows that the air chambers are long and narrow, while a cross section shows that in each flank there is one small or medium-sized chamber and in the rest of the thallus there are small or medium-sized chambers, occasionally in two, but usually in three or four stories.

5. This narrow type of thallus seems to correspond closely with Familler's "*Riccia canaliculata* (Hoffmann) Lindenberg."

6. The characteristic air chamber arrangement in each of these two types of thalli is constant whether the plants are growing in water or on land.

7. The width-thickness ratio, when used with the air chamber characteristics and the habitat, is a fairly reliable diagnostic character.

8. The narrow thalli are much less variable than are the broad thalli.

9. The narrow thalli are fertile, both in aquatic and terrestrial habitats, while the broad thalli are consistently sterile.

10. The presence of anthocyanin pigment in a thallus is not a sufficiently stable character to be used in the classification of the plant.

At this time, I wish to express my appreciation to Professor W. A. Setchell, under whose guidance this work has been carried on, for his kindly suggestions and criticism.

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Explanation of plates

Plate 4

Reproductions all life size

Fig. 1. Broad terrestrial thalli grown in small pot in window box.

Fig. 2. Broad terrestrial thalli grown in small pot in window box and then transferred to water for one month.

Fig. 3. Narrow terrestrial thalli grown in small pot in window box.

Fig. 4. Narrow terrestrial thalli grown in small pot in window box and then transferred to water for one month. (Same type as is shown in cross section, Plate I, Fig. 9.)

Fig. 5. Aquatic thalli collected at Holt, September 27, 1931. (All of these are of the broad type.)

Plate 5

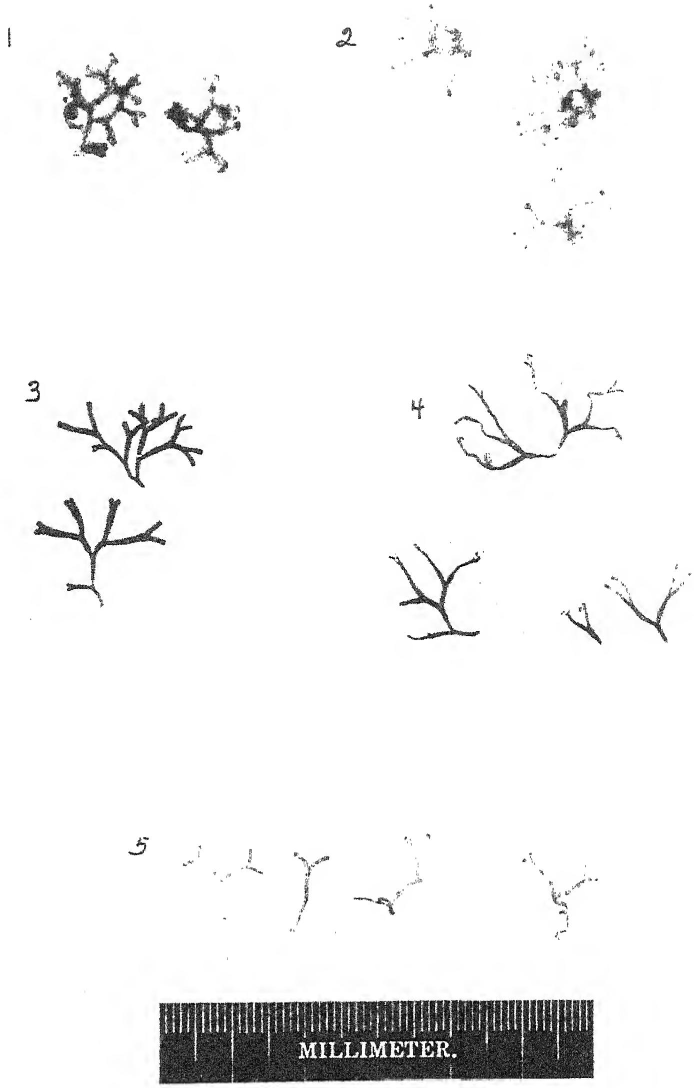
In this plate, the thalli are reduced to 0.55 of their natural size.

Fig. 1. Culture of *Riccia fluitans* collected at Holt, July 29, 1931 and grown in beaker of water in window box until September 22, 1931. It was then planted on agar where it grew until November 10th when the photograph was taken. Note that the thalli are narrower toward the base and wider towards the apices. This widening occurred after they had been planted on the agar.

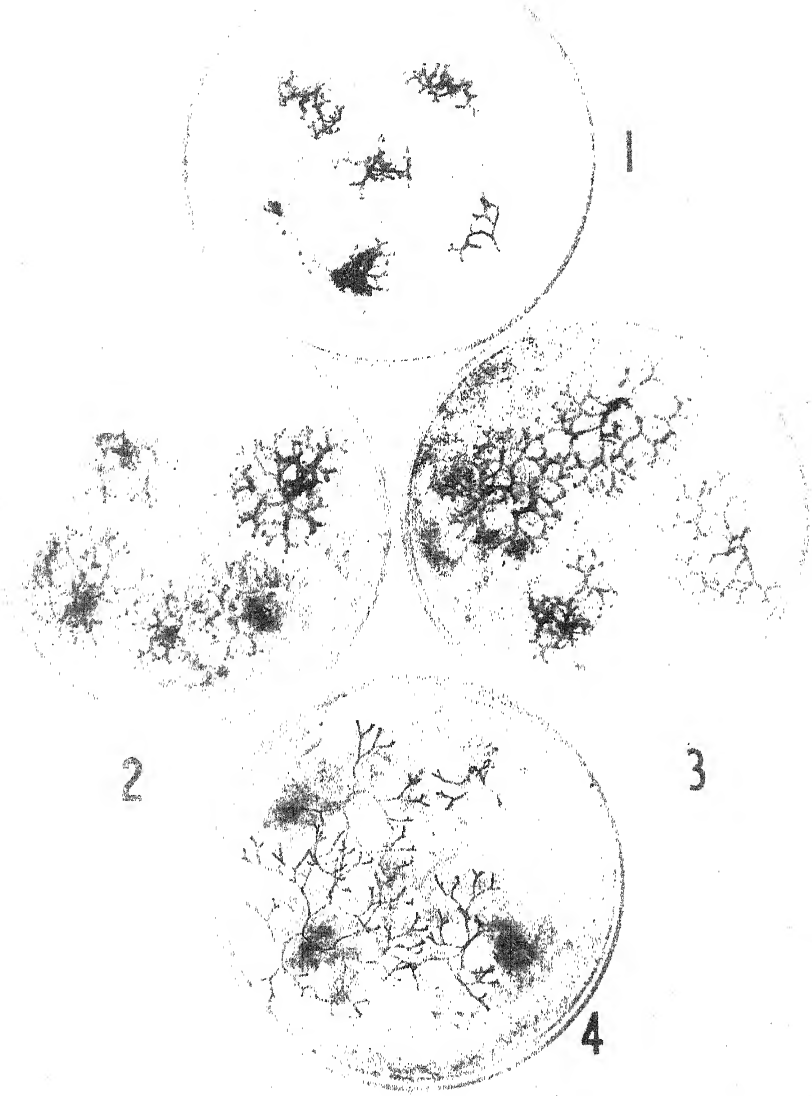
Fig. 2. Culture of wide thalli from Pot B which grew on agar from September 22 to November 10, 1931.

Fig. 3. Culture of broad thalli from Pot C. They were transferred from soil to water where they grew for twenty days. Then they were removed from the water and grown on agar for seven weeks. Note that the thalli are wide at the base, then narrow, and wide again at the apical ends.

Fig. 4. Fruiting thalli from Pot C. These were planted on agar on September 23 where they grew until November 10, 1931 when they were photographed. Note the difference in growth form of these narrow thalli from that of the wide thalli in Figs. 2 and 3.



CARTER: RICCIA FLUITANS



CARTER: RICCIA FLUITANS

A new species of Ephedra from Western Texas

E. L. Reed

In collecting plants along the escarpment and the adjacent broken lands to the east of Palo Duro Canyon, Texas, the writer collected several specimens of an *Ephedra*, vegetative structures only, which, by the available keys, were tentatively identified as *Ephedra antisyphilitica* Meyer, although differences in its habit from that species were noted. In the spring of 1932 the plants "blossomed" freely and an abundant crop of fruit was produced, the first that the writer had seen. From a careful study of the plant, its habit, its fruit, etc. it seems feasible to publish a diagnosis of it as a type of hitherto undescribed species.

Ephedra texana sp. nov. Plant a rigid, low, erect shrub, 1 to 2½ m. tall, branchlets bright green, numerous, more or less erect; scales of the twigs 2 to 6 at each node, forming a sheath 1 to 2½ mm. long, the tips obtuse, 1 to 2 mm. long or subulate, 3 to 9 mm. long; aments on short, scaly stalks; the staminate aments 5 mm. long or less; the stamen column 2 to 5 mm. long; anthers 5, 3 sessile and 2 on short filaments; bracts of the ovulate aments 5 to 6 mm. long or less; perianth lobes only slightly united; fruit an oval, red, fleshy, edible berry about 7 mm. or less in diameter; seeds ovoid, slightly triangular, exserted.

Planta: frutex humilis rigidus erectus 1–2½ m. altus; ramis viridibus numerosis plus minusve erectis; scalis ramulorum 2–6 ad quemque nodum, vagina facta 1–2½ mm. longa, apicibus obtusis 1–2 mm. longis vel sublatis 3–9 mm. longis; amentis in pedunculis brevibus squamosis, amentis masculis 5 mm. minusve longis; columna staminum 2–3 mm. longa; antheris quinque, 3 sessilibus, 2 in filamentis brevibus; bracties amentorum ovulatorum 5–6 mm. minusve longis; lobis perianthi vix coniunctis; bacca ovata, rubescente, carnosa, esculenta cir. 7 mm. crassa; seminibus ovatis, vix triangularibus exertis.

Along the escarpment and the broken country to the east from Palo Duro Canyon southward. Specimens have been collected at Quitaque, Crosbyton, Spur, Lubbock, and Post, Texas. Type locality: Buffalo Springs, Lubbock, Texas. Type specimen is in the National Herbarium, Smithsonian, Washington, D. C. This plant seems to be intermediate between *E. antisyphilitica* and *E. pedunculata*. It differs from them in the following characters: from *E. antisyphilitica* in that (a) its branches are never weak, reclining, or prostrate, (b) its perianth lobes are less united, (c) the tips of the scales are often extended into subulate awns 3 mm. to 9 mm. long, (d) two of the anthers are on short stalks and (e) the fruit is much more fleshy; and from *E. pedunculata* in that its branches are rigid and never climbing over surrounding shrubs, and (b) its aments have scaly instead of naked stalks.

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Effects of ultra-violet radiation and temperature on Fusarium

I. Lethal Action

ELIZABETH C. SMITH

(WITH TWO FIGURES)

INTRODUCTION

A study of the literature reveals a rather meager accumulation of statistical data on the effects of radiation on the fungi. This is rather surprising in view of the fact that the fungi lend themselves readily to mass methods. The literature dealing with the general and qualitative effects of radiation on fungi is, however, extensive. An attempt was made in this investigation to collect statistical data by the use of methods which were as quantitative as seemed feasible for the use of large numbers of individuals. *Fusarium eumartii* Carp. was chosen because pigment is absent in both mycelium and spores and because the size of its spores make possible rapid single spore isolations. Three aspects of radiation and temperature were considered, viz., effects of radiation on spores, effects of temperature on spores, and the relative sensitivity of spores and mycelium.

Lethal effects constitute a phase of the problem which has been given much attention and it is one of considerable interest. Writers have drawn a sharp distinction between sigmoid and logarithmic lethal curves and have given different interpretations to these two types of curves. In this paper data will be presented to show that there is a relation between the two types of curves and that possibly one interpretation will fit both types. Very little study has been previously made of either the effects of sudden changes in temperature on fungus spores or of the relative sensitivity of spores and mycelium.

EFFECTS OF RADIATION ON SPORE GERMINATION

Methods

A suspension of spores was made in sterile distilled water. The spore load (the number of spores in 1 cc. of water) was determined with a Levy counting chamber. Enough of the suspension was added to sterile distilled water to give a spore load of not more than 300. This suspension was kept at 0°C. for 12 hours. It was then plated out on potato-dextrose agar, 1 cc. of the suspension to each sterile Petri dish. The agar was prepared as follows: 200 grams of fresh potato slices were placed in 500 cc. of distilled water. The mixture was brought to a boil and then autoclaved at 15 pounds pressure for 20 minutes. A mixture of 10 grams of agar in 500 cc. of distilled water was treated in the same way. The two mixtures were then com-

bined and 30 grams of dextrose were added. The solution was diluted with distilled water to 1 liter and then filtered through cotton. Preliminary experiments with *Fusarium* cultures on potato-dextrose agar slants of different pH values had shown that 6.6. was the most favorable pH for the growth of this fungus on this medium under the usual laboratory conditions. For this reason the pH of the agar was adjusted by the colorimetric method to 6.6. The agar was sterilized in an autoclave at 15 pounds pressure for 20 minutes.

A Cooper-Hewitt mercury arc lamp operating at 7.5 amperes and 110 volts served as a source of ultra-violet radiation. The lamp was allowed to run for at least 30 minutes before each experiment so that the intensity of the radiation was fairly constant. The full spectrum of the lamp was employed. In this paper unless it is otherwise stated reference to ultraviolet so far as it is used experimentally includes some infra-red and some visible radiation. This liberty is taken with the assumption that lethal effects are due, as the extensive literature seems to indicate, to energy in the ultra-violet exclusively or practically so.

During irradiation the Petri dishes containing the spores were kept uncovered in a bath whose temperature was controlled to within 0.5°C. by a thermo-regulator. The bath was kept at 0, 10, 20, 30, 40 or 50°C. during irradiation. The Petri dishes were placed one at a time on a small metal table in the bath directly under the center of the lamp. In this way all the spores received approximately the same intensity of radiation. The distance between the lamp and the culture was 40 cm. It was found by means of a thermocouple placed on the surface of the agar in a Petri dish that less than 1.5 minutes are necessary for the agar to reach the temperature of the bath. The time necessary to produce a deflection on a galvanometer equivalent to the number of degrees difference between room and bath temperatures was always found to be appreciably less than 1.5 minutes. For this reason all Petri dishes were allowed to remain in the bath for 1.5 minutes before they were irradiated to make certain that the spores had reached the temperature of the bath.

The spores were exposed for 15, 30, 45 or 60 seconds to ultra-violet radiation, i.e., to the full spectrum of the mercury vapor lamp. Control dishes were left in the bath for 2.5 minutes so that they received a temperature treatment equivalent to that received by the spores which were irradiated for the longest period of time.

After irradiation the dishes were left at room temperature for at least 72 hours or until the spores had formed visible colonies. The time required for germination was longer after long exposures to radiation. The higher

temperatures also retarded germination. The colonies were counted, and the number of colonies was considered a measure of spore germination.

Certain preliminary experiments should be discussed to show the need or lack of need for certain precautions in the procedure. The age of the stock cultures from which suspensions were made apparently had no effect on the results obtained. Spores exposed for 12 hours to 0°C. reacted much more uniformly to radiation than spores not thus precooled. Data obtained from untreated spores were irregular and different experiments gave very different results. Experiments were made to determine, if possible, why cold treatment produced such effects. Agar plates were inoculated with 1 cc. samples from a spore suspension before and after the suspension had been treated with cold. Fewer colonies were formed from precooled spores. The spores most sensitive to cold had been killed. This fact alone, however, does not account for the leveling action of cold. The nature of the effect remains unknown. One further precaution which was deemed advisable was the use of a controlled temperature bath. Becquerel (1910) found that temperature exerts a marked effect on the susceptibility of fungus spores to ultra-violet radiation. He reported that spores of *Aspergillus niger*, *Sterigmatocystis*, and various Mucors, which without temperature control were killed in 2 to 3 minutes, resisted irradiation for 45 minutes at the temperature of liquid air. This raised the question as to what would be the effect of small temperature changes within a sub-lethal range on the reaction of *Fusarium* spores to ultra-violet.

Certain sources of error were found inherent in the procedure, and these could be minimized but never completely eliminated by careful technique. It is impossible to measure so carefully the volume of a spore suspension or to have the spores so evenly distributed in that suspension that each Petri dish will contain exactly the same number of spores. It is also impossible to determine accurately how many of those spores germinate, since the colonies are not always separate and some of the spores do not germinate until others have already formed large colonies. Theoretically, however, the percentage of spores which germinate late should be approximately the same in each Petri dish.

DATA AND RESULTS

Two types of curves commonly appear in the literature representing the death rates of organisms when the percentage of survivors is plotted as a function of the exposure to the lethal agent. In the more recent literature logarithmic curves have fallen somewhat into disrepute and the sigmoid curve is commonly thought of as the curve representing lethal rates.

Table 1 shows the effects of different exposures to ultra-violet radiation on the percentage germination of *Fusarium* spores at 0, 10, 20, 30, 40 and 50° C. The spores were kept at these temperatures only during irradiation. Following irradiation they were kept at room temperature. The germina-

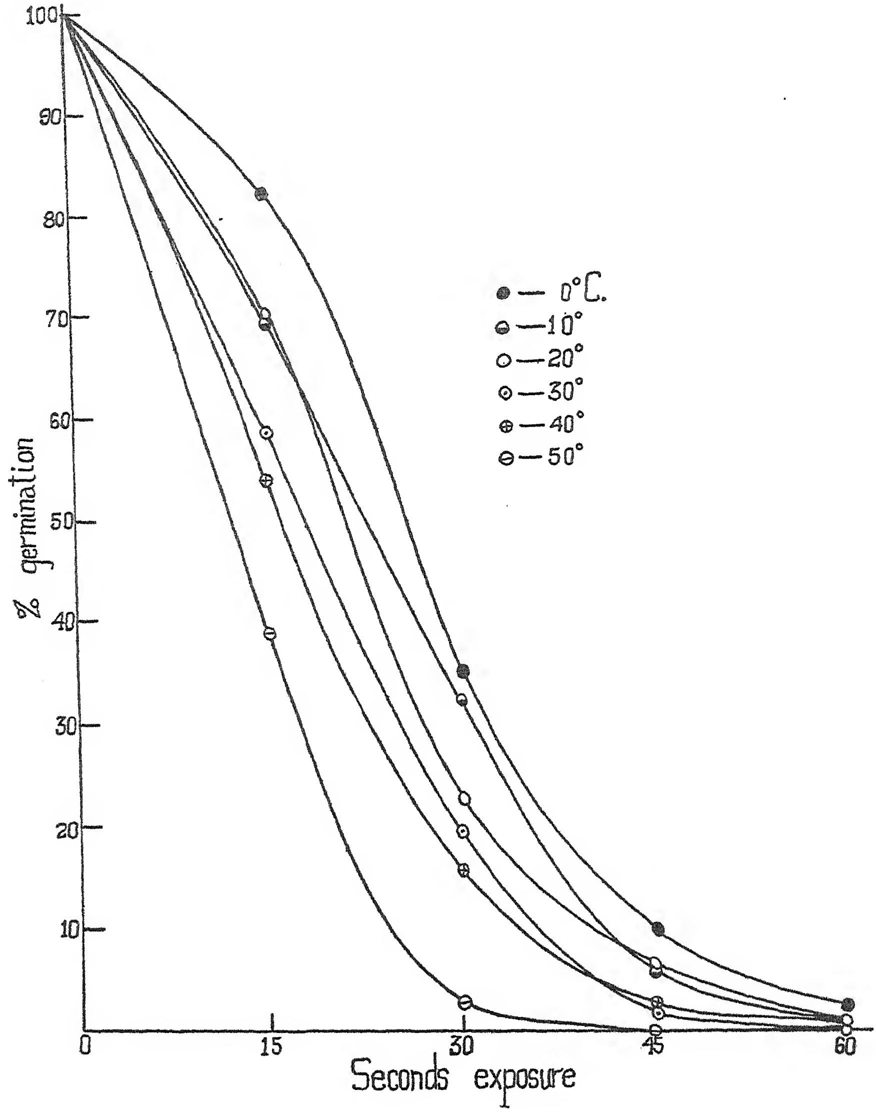

Fig. 1. The average survival of *Fusarium* spores exposed at different temperatures to ultra-violet radiation.

TABLE 1

The values given under the various exposure intervals represent average germination percentages.

TEMPERATURE, °C.	EXPOSURE IN SECONDS			
	15	30	45	60
0	80.5	35.1	9.1	2.1
10	69.3	32.3	5.5	0.6
20	72.2	22.6	6.4	0.9
30	58.6	19.2	1.4	0.0
40	53.9	15.4	2.7	0.8
50	39.1	2.9	0.0	0.1

tion of the controls is considered as 100 per cent. The table is a summary of the data from 11 experiments. An average of 60 dishes was used for an experiment and each dish contained approximately 140 spores. The results are represented graphically in figure 1. With ultra-violet as with most lethal agents deleterious action increases with a rise in temperature. The course of the lethal action follows a sigmoid curve; in other words, there is an initial period during which the death rate lags before its maximum velocity is reached. Beyond this period of maximum velocity the rate again lags and a correspondingly longer time is required to kill the remaining spores. The process of killing falls into two stages, a stage in which progressively larger numbers of spores are killed and a stage in which progressively smaller numbers of spores are killed in each unit of time. As the temperature is increased the curve tends to flatten at the upper bend and approach more and more the logarithmic type. At 50°C. the curve is essentially logarithmic. Table 2 gives the times required to kill 25 or 50

TABLE 2

The values given indicate the times necessary to kill 25 or 50 per cent of the spores at various temperatures when the time to kill 75 per cent is expressed as unity.

TEMPERATURE, °C.	25%	50%	75%
0	0.48	0.72	1.0
10	0.38	0.68	1.0
20	0.48	0.73	1.0
30	0.34	0.63	1.0
40	0.33	0.66	1.0
50	0.28	0.61	1.0
Logarithmic curve	0.20	0.50	1.0

per cent of the spores at different temperatures when the time to kill 75 per cent is expressed as unity. The times which would be required if the

curves were logarithmic are given at the bottom of the table. The observed values approximate more and more closely the logarithmic type the higher the temperature used. Table 3 is similar to table 2 except that the

TABLE 3

The values given indicate the times in seconds necessary to kill 25, 50 or 75 per cent of the spores at various temperatures. The values in parentheses indicate the times necessary when the values at 50° are taken as unity.

TEMPERATURE, °C.	25%	50%	75%
0	16.87 (3.0)	25.12 (2.0)	34.50 (1.7)
10	12.75 (2.2)	22.50 (1.8)	33.00 (1.6)
20	13.87 (2.4)	21.00 (1.7)	28.50 (1.4)
30	9.37 (1.6)	17.25 (1.4)	27.00 (1.3)
40	8.25 (1.4)	16.50 (1.3)	24.75 (1.2)
50	5.62 (1.0)	12.00 (1.0)	19.50 (1.0)

time required to kill 75 per cent of the spores is not expressed as unity. The figures in parentheses are calculated with the values at 50° taken as unity. The times required fall steadily as the temperature is increased. It takes 3 times as long to kill 25 per cent of the spores at 0°C. as it does at 50°C. As the temperature is increased the death rate increases more rapidly in the upper part of the curve than in the lower part and thus tends to reduce the sigmoid character.

A somewhat similar experiment was performed by Gates (1929) with ultra-violet light on bacteria. He found that when he irradiated *Staphylococcus aureus* with 2540Å at 5, 21 and 36°C. deleterious action increased with a rise in temperature and that the curves were all sigmoid.

The question arises as to the possible significance of lethal curves. Rahn (1929) stated that "the order of death is not a function of the killing agent but a property of the organism since so many different agents produce similar curves". J. H. Smith (1921) obtained curves showing the action of various concentrations of phenol on *Botrytis* spores, which resemble very closely the curves described here. On the other hand, curves in which he substituted heat for phenol show no tendency to approach the logarithmic type (Smith, 1923). This strongly suggests that all killing agents do not act alike and that in at least some respects the action of ultra-violet radiation on spores at different temperatures is more like the action of phenol than that of heat. Smith was able to obtain true logarithmic curves if he used young spores, which he found are more sensitive than older ones to low concentrations of phenol. Thus both logarithmic and sigmoid curves are characteristic of death rates. It is somewhat surprising

that such a wide variety of lethal agents as have been employed (heat, chemicals, ultra-violet, etc.) should produce death rates which correspond to one of these two types of curves. Rahn's statement that "the order of death is not a function of the killing agent" holds in some measure. With curves such as those of Smith with phenol and those presented here, the idea of the logarithmic and sigmoid types as something distinct gives way to the conception of a gradual transition between them.

The logarithmic type of curve is characteristic of monomolecular reactions, and consequently it has been considered by those favoring the logarithmic curve that death results from some type of monomolecular reaction. Those who favor the sigmoid type have attributed the character of the curve to chance variation in resistance. These two somewhat opposing views have been fully reviewed and defended by Brooks (1906) and by Cohen (1922). A symmetrical sigmoid curve, when transformed, becomes a normal frequency curve such as would result from chance variation. It seems unlikely that some entirely different factor should be responsible for the logarithmic curve, and the possibility exists that the resemblance between the logarithmic lethal curve and the monomolecular curve is entirely fortuitous. The resemblance likewise between the normal frequency curve and the similar curve obtained from the sigmoid type may, of course, also be fortuitous. It has been suggested that if the latter is the case the logarithmic is the typical death rate curve, and that while departures from it may be due to individual variation the fundamental nature of the curve is due to something quite different, perhaps to the fact that death is characterized by some monomolecular reaction. The other course which is open, and which seems to the author as involving less speculation, is that the fundamental nature of the curve is due to individual chance variation and is therefore sigmoid in shape. The logarithmic curve results only when the treatment is so rigorous that all of the more sensitive individuals die almost instantaneously, at least so rapidly that measurements are not sufficiently fine to detect any differences in resistance. Carrying this idea still further it is easy to conceive of a treatment so promptly lethal that all of the spores would be killed before any intermediate stages could be detected. The logarithmic curve is merely a sigmoid curve with the upper part very much flattened. Table 3 shows that with high temperatures the time of killing is much more reduced in the early part of the process than in the later stages. This would not necessarily be the case with high intensities of all types of killing agents, so that the logarithmic curve is not always characteristic of strong lethal action.

Many experiments made by others have shown that the effects of exposures to ultra-violet radiation are usually additive. For example, 2 one-

minute exposures to "x" intensity produce the same effect as 1 one-minute exposure to "2x" intensity. The total effect may depend, as it does in many photochemical phenomena in the purely physical world, on the total number of light quanta which are absorbed by the individual. If this is true then any particular spore will die when the necessary number of quanta of ultra-violet radiation have been absorbed. The time can be reduced by increasing the intensity or by decreasing the resistance of the spore. In the experiments described here the resistance was decreased by increasing the temperature.

By way of summary, the death rates of *Fusarium* spores exposed to ultra-violet radiation at different temperatures take the form of sigmoid curves which rapidly approach the logarithmic type as the temperature is increased. Deleterious action increases with a rise in temperature. As the temperature is increased the death-rate increases more rapidly in the upper part of the curve than in the lower part. The significance of such curves is still somewhat obscure, but it seems probable that chance variation in resistance to the lethal agent is responsible for the shape of the curves. Those curves which approach the logarithmic type are merely modified sigmoid curves in which the lethal rate has increased most for the least resistant spores. A rise in temperature increases spore sensitivity, and there is also the possibility that temperature may sometimes act as a lethal agent in conjunction with ultra-violet radiation.

TEMPERATURE COEFFICIENTS

The use of temperature coefficients often gives the biologist some insight or clue to the nature of the reaction which he is studying. The question immediately arises as to whether the reaction which manifests itself in the sigmoid lethal curve is primarily of a physical or chemical nature. A temperature coefficient is defined here as the ratio of the times required to reach a constant result with a 10° rise in temperature. Table 4 gives temperature coefficients calculated for different portions of the lethal curves presented in figure 1. Since the 10° and 20° curves cross, probably because the technique is not sufficiently accurate to separate the two curves, some blanks appear in the table. These coefficients would be negative if calculated, and since such coefficients are unlikely to occur it is assumed that they are incorrect. The rest of the values, however, are quite constant. The average temperature coefficient for 0 to 40° is 1.13 and for 40 to 50° is 1.37. These temperature coefficients are characteristic of a physical or photochemical reaction rather than of a purely chemical reaction. This suggests that death may be a direct result following the absorption of energy.

These temperature coefficients are in quite close agreement with the temperature coefficient of 1.05 obtained by Bayne-Jones and Van der Lingen (1923) for bacteria exposed to the total radiation of a zinc spark and also to that of 1.09 obtained by Gates (1929) for *Staphylococcus aureus* exposed to 2540Å. They differ markedly from those of J. H. Smith (1923) for the action of heat on *Botrytis* spores. He obtained values ranging from 29.5 to 690.0, the highest temperature coefficient being representative of

TABLE 4

Temperature coefficients calculated for different portions of the lethal curves.

PERCENTAGE KILLED	SECONDS REQUIRED TO KILL						TEMPERATURE COEFFICIENTS				
	DEGREES C.						DEGREES C.				
	0	10	20	30	40	50	0–10	10–20	20–30	30–40	40–50
10	9.0	6.7	5.6	4.4	3.1	2.0	1.33	1.20	1.27	1.38	1.54
20	15.0	9.9	11.6	7.5	6.5	4.5				1.14	1.45
30	18.7	14.6	15.7	11.2	9.7	6.7				1.15	1.44
40	21.7	18.7	18.1	14.6	12.9	9.3	1.16	1.03	1.24	1.13	1.37
50	25.1	22.5	20.8	17.6	16.3	12.0	1.11	1.07	1.18	1.07	1.36
60	28.3	26.6	23.6	20.4	18.7	14.8	1.06	1.12	1.15	1.08	1.26
70	32.2	30.7	26.8	24.3	22.5	18.0	1.04	1.14	1.10	1.08	1.25
80	37.3	35.2	31.8	29.2	27.3	21.0	1.05	1.10	1.08	1.06	1.30
							1.12	1.11	1.17	1.13	1.37 Av.

the lowest temperature. If a high temperature coefficient, which Smith has demonstrated to be characteristic of a heat effect, is due to a heat effect here, then this study of temperature coefficients may show that between 40 and 50°C. temperature acts not merely as a sensitizer but also as a lethal agent in conjunction with ultra-violet radiation.

TEMPERATURE EFFECTS

In order to study the effects of sudden changes of temperature on *Fusarium* spores sterile glass capillaries approximately 1 to 1.5 millimeters in diameter and 7 to 8 inches in length were partially filled with a heavy spore suspension and sealed in an alcohol flame. The capillaries were weighed before and after filling to determine the weight of the spore suspension in each capillary. The capillaries were then immersed in a bath at temperatures ranging from 0 to 52°C. for periods of 30 seconds to 10 minutes. Duggar[1] found by use of a small thermo couple that solutions contained in glass capillaries of these dimensions reach the temperature of the bath almost instantaneously. By the use of this method the spore suspension can be brought to any desired temperature without an ap-

[1] Duggart, B. M. (*Inedit.*) Determination of inactivation temperatures with plant viruses.

preciable time-lag. After exposure the capillaries were immersed immediately in dilute hydrochloric acid at room temperature. This brings the spore suspension quickly back to room temperature and also kills bacteria which may be present on the outside of the capillaries. Then, under the protection of a sterile transfer chamber, the ends of the capillaries were broken and the spore suspension from each was plated out separately on agar prepared as before. One cubic centimeter of sterile distilled water was added to each Petri dish so that the spores might be spread more uniformly over the agar. Colony counts were made after about 72 hours, and the number of colonies was considered a measure of spore germination. The percentage germination was calculated by comparing each germination with that calculated for an equal weight of a control suspension. The method outlined here is tedious, contaminations frequently occur, and spores adhering to the inner walls of the capillaries introduce a rather large source of error. In any one experiment, however, repetitions of any particular temperature treatment gave fairly constant results, but repetitions of the experiment with a different spore suspension gave widely different results. This was true even if precautions were taken to use spores of approximately the same age and to have all other conditions as nearly uniform as possible.

The only conclusions which can be drawn are that the spores are extremely variable in their response to sudden changes of temperature and apparently very slight variations in previous environment have much to do with their behavior. With temperatures above 48°C. there is always some lethal action which increases rapidly with slight increases in temperature.

A study was also made of the effects of temperature changes on spores plated on potato-dextrose agar. The plates were placed in a bath at 0, 10, 20, 30, 40 and 50°C. for 2.5 minutes. It requires approximately 1.5 minutes for the spores to reach the temperature of the bath whereas the change in temperature is almost instantaneous when the spores are in capillaries. But here again the results are just as variable. In one experiment the number of spores which germinated continually increased with an increase in temperature. In another it continually decreased, while in others the maximum germination occurred at some intermediate temperature.

The action of temperature alone must not be confused with its action in conjunction with ultra-violet radiation. The two are strikingly different. In the study of the lethal effects of ultra-violet on spores irradiated at different temperatures the values which were used to calculate the averages indicated in table 1 never varied more than 10 per cent despite the fact that no attention was given to the age of the spores used.

SENSITIVITY

The mycelium of fungi is in general more sensitive to ultra-violet radiation than the spores. To study the relative sensitivity of the spores and mycelium of *Fusarium* to ultra-violet radiation the spores were placed in sterile distilled water and 1 cc. samples of the suspension were plated out on agar prepared as for the study of lethal action. Once every hour 5 to 10 plates were exposed to ultra-violet at 0°C. at 40 cm. from the lamp. To study the effects of radiation on spores and mycelium in different stages of development it was necessary to use several spore suspensions made at different times preceding irradiation. Because of the nature of the experiment the precooling treatment employed in other phases of this work had to be omitted. This resulted in much more variable results than were obtained in the study of lethal action. The exposure was for 15 seconds in experiment 1 and for 30 seconds in experiments 2, 3 and 4. Approximately

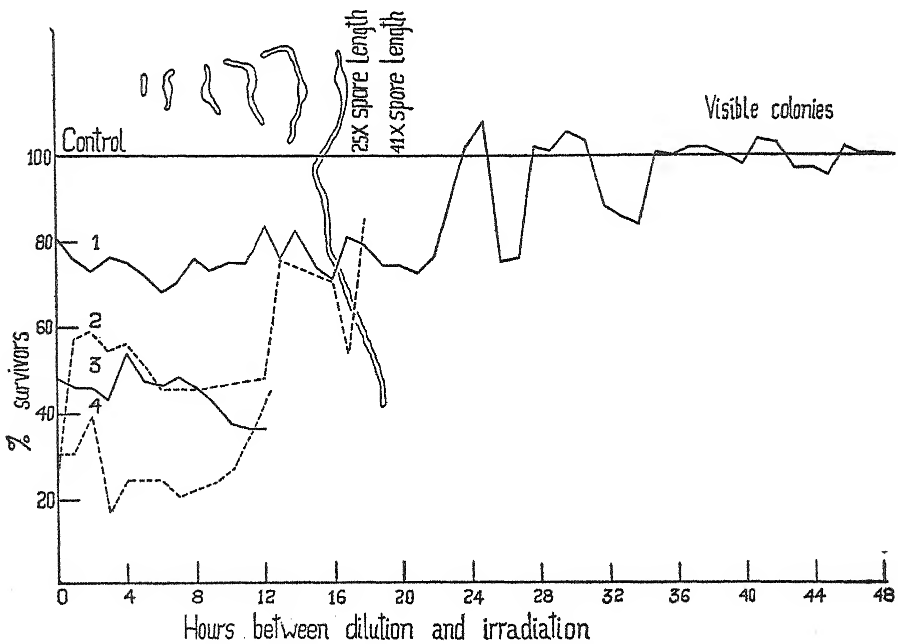

Fig. 2. The relative sensitivity of the mycelium and spores of *Fusarium* to ultra-violet at 0°C. After a suspension was made the spores were irradiated at one hour intervals. The different stages of development at the time of irradiation are indicated above their proper horizontal coordinates.

72 hours after the suspension was made the colonies were counted. The results are shown graphically in figure 2 with the number of hours between

dilution and exposure plotted against the percentage of survivors. During the course of the experiments camera lucida drawings were made of the spores and mycelium at various stages of development and these are reproduced in the graph above their proper horizontal coordinates. The spores germinated at approximately the same time in all four experiments. Experiment 1 was designed to show the relation between the sensitivity of the mycelium and the spores. While a 15-second exposure kills about 20 per cent of the spores it has little to no effect on the mycelium. In other words, the spores are more sensitive than the mycelium to ultra-violet radiation. This experiment also suggests that the germinating spore is no more sensitive than the resting spore. Experiments 2, 3 and 4 verify this suggestion. Both of these results are, in general, contradictory to those which have previously been reported for fungi. Schulze (1909) reported that the mycelium of *Mucor stolonifer* is more sensitive than the spores to ultra-violet radiation of 2800Å. Fulton and Coblentz (1929) found that the mycelia of *Penicillium digitatum* and *P. italicum* are more sensitive to ultra-violet radiation than are the spores. Elfving (1890) found that germinating spores of various fungi are much more sensitive to sunlight than are the resting spores. Neidhart (1924) reported that germinating spores of *Sporotrichum Beurmanni* are three times as sensitive as are the resting spores to X-rays or radium. Previous results then indicate that the mycelium is more sensitive than the spores and that germinating spores are more sensitive than resting spores. But with *Fusarium* the spores are more sensitive than the mycelium and the germinating spores are no more sensitive than the resting spores. Chavarria and Clark (1924) have stressed the protective action of pigment against the harmful effect of ultra-violet radiation. This suggests the idea that in forms which have spores with more pigment than the mycelium one might expect that the mycelium would be more sensitive than the spores. The fungi mentioned above, however, represent all kinds of variations in pigmentation so that some other factor must determine sensitivity. This does not imply that pigment has no effect but merely that some other factor must be assumed to explain the data which have accumulated on sensitivity.

SUMMARY

1. The death rates of *Fusarium* spores exposed to ultra-violet radiation at different temperatures take the form of sigmoid curves which rapidly approach the logarithmic type as the temperature is increased. Deleterious action increases with a rise in temperature. The theory is advanced that sigmoid curves are due to chance variation in resistance to the lethal

agent and that logarithmic curves are merely modified sigmoid curves in which the death rate has increased most for the least resistant spores.

2. The average temperature coefficient between 0 and 40°C. is 1.13 and between 40 and 50°C. it is 1.37. These coefficients are characteristic of a physical or photochemical reaction. The higher temperature coefficient between 40 and 50°C. may indicate that temperature has not merely a sensitizing effect but also a lethal effect in conjunction with ultra-violet radiation.

3. The effects of temperature are variable in the absence of ultra-violet radiation but relatively constant in the presence of it.

4. The mycelium of the fungus used is less sensitive to ultra-violet than the spores, and germinating spores are no more sensitive than resting spores.

This investigation was proposed by Prof. B. M. Duggar and has been carried on with his suggestions and criticisms. The author is indebted to Prof. Duggar and to Prof. H. H. Bartlett for assistance in the preparation of the manuscript. The latter part of this investigation was carried on at the University of Michigan with the aid of an F.C. and Susan Eastman Newcombe Fellowship.

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INDEX TO AMERICAN BOTANICAL LITERATURE
1931–1934

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A fossil Cochlospermum from northern Patagonia

Edward W. Berry

(with two text figures)

The genus *Cochlospermum* of Kunth comprises a variety of forms mostly referred to *Maximilianae* Martius and Schrank and formerly included in the family Bixaceae of the order Parietales. More recently *Cochlospermum* and the small genus *Amoreuxia* (*Euryanthe*) have been constituted as a separate family—the Cochlospermaceae, and along with the families Bixaceae, Flacourtiaceae, Samydaceae, Canellaceae and Cistaceae, have been segregated from the Parietales as an independent order: the Bixales.

In examining a large collection of fossil plants from the Miocene of northern Patagonia[1] an undoubted species of Cochlospermum was encountered. This comes from the valley of the Rio Pichileufu about thirty miles east of Lago Nahuel Huapi in Latitude 41°10′ south and Longitude 70°52′ west in Rio Negro Territory.

The fossil species is named from its similarity to a recent tropical American species, and may be described as follows:

Cochlospermum previtifolium Berry, n.sp.

Leaves large, palmately 5 to 7 lobed. Lobes varying from lanceolate to ovate, separated by rather narrow rounded sinuses extending half way to the base or farther. Central lobe the same size or wider than the lateral lobes. Base cordate. Tips acuminate. Margins varying from nearly or wholly entire to remotely serrate to closely dentate. Texture subcoriaceous. Length varying from 12 to 22 centimeters. Maximum width varying from 16 to 33 centimeters. Petiole long and very stout, not complete in any specimen, but preserved for lengths up to 11 centimeters. The primaries diverge at acute angles from the top of the petiole, are stout and prominent and run as midveins to the tips of the lobes. The secondaries are well marked, but neither especially stout nor prominent. In the lobes they diverge at angles of more than 45 degrees at fairly regular intervals, and are curved ascending and camptodrome or partly or wholly craspedodrome, depending on the entire or toothed character of the margin. Where the marginal teeth are widely spaced they tend to be the same number as the corresponding secondaries, but in those cases where the teeth are closely spaced the secondaries are ½ or fewer in number than the teeth and the secondaries then send out one or more outer laterals to the supernumerary teeth. In the undivided part of the leaf the secondaries become more irregularly spaced and straighter, and anastomose in a variety of ways. In all

[1] Berry, E. W. Proc. Natl. Acad. Sci. **20**: 280–282, 1934.

[The Bulletin for January (62: 1–64) was issued January 3, 1935]

cases observed a continuation or branch of the secondaries from adjacent mid-veins forms a marginal hem around the included sinus. The tertiaries are thin and not well displayed; they are nearly straight and percurrent where the distance to be spanned is small, but anastomose in the middle region where the distance is greater.

Fig. 1. Cochlospermum previtifolium Berry.

This species is one of the most common in the Rio Pichileufu collections but because of the large size of the leaves there are no complete specimens. This does not appear to be due to any incompleteness at the time of their burial, but seems to be due entirely to breakage in splitting them out of the tufaceous matrix. I have seventeen specimens representing every part of the leaf, and instead of figuring actual specimens I have assembled in the accompanying figure actual variations in size, shape, marginal features and venation such as occur on different leaves. Any single leaf is to be understood as having all five or seven lobes of the same character as one of the lobes of the restoration except that in entire margined leaves there may be a few widely spaced teeth in the distal part of the central or the first lateral lobes.

As can be seen the species is well characterized, and although there are suggestions of malvaceous or aralioid resemblances, the fossil material

agrees so closely with the recent American species of *Cochlospermum* that I have no hesitation in so identifying it. Making assurance doubly sure is the presence of a specimen and counterpart of a subspherical capsular fruit with a stout peduncle preserved for a length of $3\frac{1}{2}$ centimeters, which had dehisced before or was crushed during burial, which shows the impression of the silky fibres associated with the seeds. This capsule is about 3.75 centimeters across and as far as its features are perserved it agrees so perfectly with the recent fruits of *Cochlospermum* that I feel entirely justified in referring it to the same botanical species as the leaves.

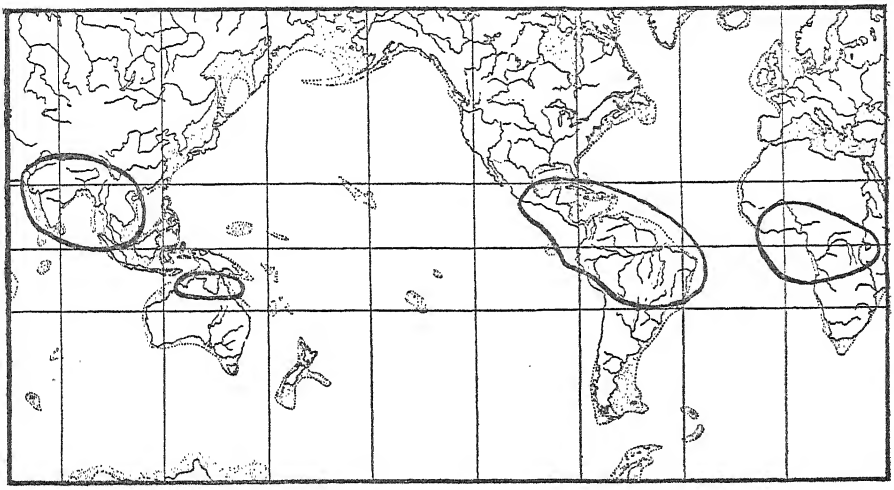

Fig. 2. Distribution of the genus Cochlospermum.

The fossil is very similar to and may well be the ancestor of the living *Cochlospermum vitifolium* (Willdenow) Krug, a shrub or small tree widely distributed in the American tropics where it ranges from Mexico through Central America, the West Indies and northern South America to eastern Bolivia and central Brazil. I have seen recent material from all of these regions and it may well be that the species extends southward into Paraguay and the humid tropical part of northern Argentina.

The genus has a most interesting and disconnected distribution which I have shown roughly on the accompanying sketch map. There are thirteen or more species in the recent flora: three in northern Australia, four in Africa and Asia, and six in tropical America. If these all belong to a single genus this is a certain indication of an extended geological history. In so far as the leaves are concerned the Old World species are not at all closely similar to the American species.

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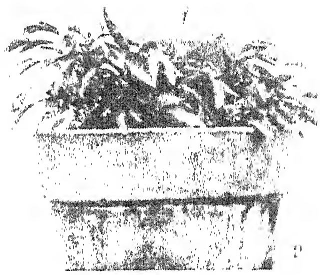

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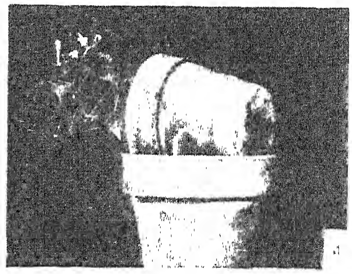

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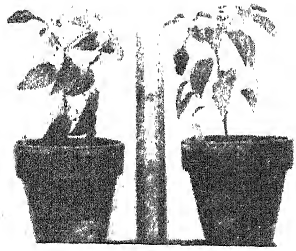

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KAISER: GEOTROPIC RESPONSE

Cytological aspects of Grindelia species

THOMAS W. WHITAKER AND JULIAN A. STEYERMARK

INTRODUCTION

The genus *Grindelia*, indigenous only to North and South America, comprises 58 species, of which 45 are North American, in addition to a multitude of varieties and forms.[1] Taxonomically the genus, like *Viola*, *Dodecatheon*, *Crataegus*, *Salix*, and *Rubus*, is a very natural one; but, as in the case of such homogenous well-defined genera, the species of *Grindelia* are very closely inter-related, and often difficult to distinguish from one another. With such closely-knit groups, it is highly desirable, in dealing with evolutionary and inter-specific problems, to have as much supporting data as possible from several fields of botanical endeavor, such as cytology, genetics, and anatomy. It therefore seems advisable to record certain aspects of the subject, of which the present paper represents a preliminary treatment.

In *Grindelia*, the evolutionary history has been found to be closely correlated with the geographical distribution and limitations of the various entities; furthermore, the gaps in the phylogenetic tree are relatively few, because the species are closely related, and the continuity of derivation of one entitiy from another is rather evident. The closely related species in the phylogenetic treatment of the genus have been found to be geographically proximate, and either overlap in the marginal portions of their geographic ranges, or occupy areas not very remote from one another. Thus one can trace in *Grindelia* a phylogenetic sequence which is directly correlated with a geographical sequence based upon study of the past geological history of the areas concerned.

The majority of the species of *Grindelia* are recently evolved youthful types, merely beginning, and have had their origin only in Pleistocene or Post-Pleistocene times; they occur on territory such as drowned river valleys of the Pacific Coast, youthful river alluvium of the San Joaquin and Sacramento River regions, Quaternary lava deposits, etc. On the other hand, there are within the genus, species of a more ancient dispersal which occupy land areas which have stood above sea-level or escaped glaciation since the close of the Paleozoic (as in the Ozark Plateau), or since the close of the Cretaceous (as in the Mexican Plateau or Edwards Plateau of Texas). The species of *Grindelia* limited to such geologically older territory are regarded as of a more ancient dispersal than those occurring on ter-

[1] Steyermark, J. A. 1935. A monograph of the North American species of the genus *Grindelia*, Ann. Mo. Bot. Garden.

ritory available only recently. These species of a more ancient geological dispersal have been placed near the lower portion of the evolutionary tree, and are treated as ancestral or quasi-ancestral types. Certain primitive morphological characters—as erect or spreading, rather than revolute, involucral bracts—are associated with these more primitive Mexican, Texas, and Ozarkian species.

MATERIALS AND METHODS

The cytological data in this report are based primarily upon the study of somatic chromosomes in root-tip material. During the summer of 1933 the plants were set out-of-doors, and pollen mother cell material and pollen sterility counts were secured on the plants that flowered before the onset of heavy frost in the fall of 1933. In all, 12 species, including 3 varieties, were studied cytologically.

Grindelia is difficult cytological material. The chromosomes are small and, while they are not numerous, they are contained in relatively small cells. Owing to the milky, sticky substance which must be overcome when dealing with the flowers, it is extremely difficult to obtain proper fixation of the pollen mother cells. When making aceto-carmine smears, the sticky secretion is a great obstacle to successful smearing. The material collects in round, gummy masses, which hinders effective flattening under the cover glass. However, the best slides for the study of meiosis were secured from aceto-carmine smears.

In an effort to dispose of the sticky substance, the flowers were dissected into small masses and fixed in aceto-alcohol for 24 hours and then smeared and stained with aceto-carmine. This treatment was successful in disposing of the sticky substance, but the chromosomes seemed to have a tendency to clump after this treatment, especially in the tetraploid species. Apparently clumping was due to the sticky substance impeding the penetration of the fixative.

OBSERVATIONS

Table 1 summarizes the cytological data obtained in this study.

Obviously, all the 14 types of *Grindelia* represented in this study are either diploids or tetraploids. This situation is to be expected in perennial species chiefly propagated by sexual means. Triploids and plants with abnormal chromosome complements (monosomics, trisomics, etc.) are generally less vigorous and fertile than diploids or tetraploids, and would be eliminated, whereas in species capable of vegetative reproduction there would be tremendous increase in their chance of survival.

TABLE 1

	PLANT NO.	SPECIES	CHROMOSOME NO. (n)	(2n)	% OF POLLEN STERILITY
Diploids	24	*G. columbiana*		12	
	31	*G. decumbens*		12	
	70	*G. lanceolata*		12	
	28	*G. nana*		12	
	27	*G. perennis*		12	
	8	*G. procera*	6	12	5
Tetraploids	10	*G. camporum*	12	24	13
	50	*G. hirsutula* var. *brevisquama*		24	
	56	*G. humilis*		24	
	1	*G. maritima*		24	
	61	*G. rubricaulis* var. *elata*	12	24	6
	3	*G. rubricaulis* var. *platyphylla*		24	
	15	*G. squarrosa* var. *nuda*	12	24	17
	5	*G. arenicola* x *G. rubricaulis* var. *platyphylla*	12	24	25

The chromosomes in *Grindelia* are slender curved rods of approximately equal length. They appear to have median attachment constrictions. Because of the difficulty in fixation, critical evidence as to whether there was secondary pairing in the tetraploids could not be obtained.

With one exception (No. 5) the meiotic divisions proceeded in the normal fashion. There was not an exceedingly high percentage of pollen sterility in the species studied. The high percentage of good pollen is an indication that meiosis is perfectly regular. In No. 5 there is considerable evidence of irregularities during meiosis. Lagging, lack of pairing, etc., were observed. The pollen sterility is comparatively high in this species (25%).

DISCUSSION

A striking correlation is brought out when these species are studied in the light of their phylogenetic history. Some of the diploid types of *Grindelia*, such as *G. lanceolata*, *G. decumbens*, and *G. procera*, are species which, from a phylogenetic standpoint, are either of a more ancient dispersal, occurring on geologically older territory, such as *G. lanceolata* of the Ozark region, or are regarded as near certain ancestral or primitive types. For example, *G. decumbens*, a diploid, is closely allied to *G. arizonica* which is a species near the beginning of a group of primitive species. *G. procera*, also a diploid type, is closely allied to the most primitive California species—namely, *G. Halli*. This latter species has been derived from *G. arizonica*, which, in turn, has descended from Mexican types similar to

G. oxylepis. Thus, *G. procera*, one of the more primitive Californian types, exhibits in its diploid nature its primitive heredity harking back to the more ancient Mexican stock.

On the other hand, when the tetraploid entities are examined, we find that they are all species occurring on territory which is geologically more youthful, and, as such, are of a more recent dispersal. Most of them are the most recently evolved Californian types which have been derived from diploid heritage, found, for example, in *G. procera*. We find a striking case of apparent derivation that has taken place from *G. procera* to *G. camporum*. The latter is a tetraploid type, whereas the former is a diploid. In its small heads, semi-erect or ascending, short-tipped involucral bracts, and short pappus-awns, the diploid *G. procera* is obviously related to the most primitive of Californian Grindelias, namely, *G. Halli*. Upon leaving an area in Southern California near the region where *G. Halli* occurs, and following northward along the San Joaquin River valley, *G. procera* has given rise, near its northern limit, to *G. camporum*, a tetraploid. This derivation is in perfect accord with the sequence of geographical migration northward and with the development of certain morphological characters carried to a more pronounced degree of development. Thus, the tetraploid, *G. camporum*, appears to be an enlarged and more robust edition of *G. procera*. *Grindelia camporum* has differentiated from *G. procera* by an enlargement of the heads from 1.1–1.8 cm. broad to 1.5–2.5 cm. broad, increasing the size of the achenes from 2–4 mm. long to 3.5–5.5 mm., lengthening the tips of the involucral bracts from 2–3 mm. long to 4–7 mm.; moreover, in *G. camporum*, the involucral bracts have become more resinous, firmer, and more spreading; the awns have become stouter; the disk florets larger; and a greater resin output is present in the leaves.

From the preceding evidence, it would appear that some of the diploid species so far studied, such as *G. lanceolata*, *G. procera*, and *G. decumbens*, are the most primitive, and that the tetraploid ones are more recently evolved, and have descended, in some cases at least, from diploid stocks.

It is also probable that certain tetraploid species, such as the majority of the closely related Californian species, as *G. humilis*, *G. maritima*, and *G. rubricaulis* and varieties, may have descended from tetraploid stocks, and, in turn, as well, may have given rise to subsequent tetraploid types.

The collection denoted in Table I as No. 5, was taken near Pigeon Point, San Mateo Co., California. Morphologically and taxonomically this collection appears intermediate between two entitites, i.e., *G. rubricaulis* var. *platyphylla* and *G. arenicola*, and it is difficult to place definitely with either the one or the other. Some of the No. 5 collection have the procumbent to spreading habit of *G. arenicola*, whereas others have the semi-

erect to almost erect habit typical of *G. rubicaulis* var. *platyphylla*. The basal and lower cauline leaves resemble those of *G. arenicola*, but the main middle and upper cauline are mostly broadly oblong and subtruncate or obtuse at the apex, as in *G. rubricaulis* var. *platyphylla*. The stems do not arise from spreading subligneous axes as in *G. arenicola*, but directly from herbaceous bases. Further, the serrulate margin of the pappus-awns suggests the *G. arenicola* ancestry. But more than this evidence, the geographical relationships of these two entities are important. *G. rubricaulis* var. *platyphylla* occupies a limited coastal area, occurring most typically in Monterey Co., but it is found scattered north to Marin Co., and locally south on some of the Santa Barbara Islands. *G. arenicola* occurs typically along the coast from Coos Co., Southern Oregon, south along sand dunes and flats in Northern California where it is typical, but extends southward to Cypress Point and Carmel on sand dunes in Monterey Co., and locally still farther south on Santa Rosa Island. Near or at the marginal portions of the ranges of these two entities, where this overlap in natural range occurs, appear these intermediate types, puzzling and difficult to place taxonomically. A number of such collections have been made in Monterey and San Mateo counties, which from a taxonomic-morphologic-phytogeographic viewpoint would be regarded as natural hybrids. It is, therefore, interesting to find, when No. 5 is studied cytologically, that there is evidence of a considerable amount of irregularity in the meiotic divisions. There is some lagging on the part of several bivalents, precocious division, lack of pairing, etc. The rather high pollen sterility can be accounted for by these observations at meiosis. This sort of cytological behaviour seems to be typical of some species hybrids. We may, therefore, say with some confidence that No. 5 represents from a cytologic, taxonomic, morphologic, and phytogeographic viewpoint, a natural hybrid.

SUMMARY

1. Chromosome number in twelve species and three varieties of *Grindelia* has been reported. The basic chromosome number in this genus is 6. The species examined were diploid and tetraploid in about equal numbers.

2. A close correlation exists between the cytological data and the phytogeographic dispersal of the species.

3. Evidence from several sources indicates that one of the entities examined may be a natural hybrid (*Grindelia arenicola* × *G. rubricaulis* var. *platyphylla*).

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The inheritance of a geotropic response in Capsicum fruits[1]

SAMUEL KAISER

(WITH PLATE 6)

Pendent-fruited and erect-fruited varieties of the red pepper, *Capsicum annuum*, have long been known. This difference in fruit position has been used as a diagnostic character in the classification of the species by Fingerhuth and Dunal (Irish, 1898). In the former type, the fruit stalk at maturity is recurved and pendent so that the stigmatic end of the fruit points downward (fig. 1); in the latter, the mature fruit stalk is vertical and erect, the tip of the fruit pointing upward (fig. 2).

The inheritance of this character difference has been studied by Webber (1912), Ikeno (1913) and Groth (1913, 1914). In general, their results show that the pendent type tends to be dominant over the erect and that the F_2 plants segregate in a monohybrid ratio. Indefinite and somewhat conflicting reports of an intermediate condition found among the progeny of pendent and erect plants are made by these authors.

The present paper presents evidence that this difference in position of the mature fruit is due primarily to a single gene difference and that this genetic determination operates through a specific geotropic growth response.

BREEDING BEHAVIOR

In the course of an investigation concerning the factors governing size and shape in pepper fruits, a number of crosses were made involving pendent and erect plants. These plants had been inbred for several generations and the fruit positions in both had invariably remained true to type. In ten such crosses pendent plants were used as seed parents, in five as pollen parents. The hybrids from these reciprocal matings resembled without exception the pendent parents in the position of the mature fruits (fig. 3). No intermediate types were observed. Four hundred and two F_2 plants[2] were grown from five of these hybrids. Each plant was checked for pendent-erect classification after most of the fruits had ripened. The results are shown in table 1. In general, considering the entire F_2 population, the ratio between pendent and erect types approximates 3:1, but several exceptions

[1] Contribution No. 10, Department of Biology, Brooklyn College.

[2] These plants were grown during the summers of 1932 and 1933 at the Brooklyn Botanic Garden and at the State Institute of Applied Agriculture on Long Island. The writer is grateful to Dr. G. M. Reed and to Director H. B. Knapp of these respective institutions for their kind assistance.

TABLE 1

F_2 Segregation for pendent and erect fruit position
(Lines 1, 8 and 32 are pendent types; lines 5, 9 and 24 are erect)

	ALL FRUITS PENDENT		MOST PENDENT, SOME ERECT		ALL FRUITS ERECT		MOST ERECT, SOME PENDENT		FRUIT POSITION INTERMEDIATE		TOTALS
	NO.	%	NO.	%	NO.	%	NO.	%	NO.	%	
8× 5	61	67.8	7	7.8	21	23.3	0	0.0	1	1.1	90
8× 9	59	72.0	6	7.3	17	20.7	0	0.0	0	0.0	82
8×24	36	61.0	6	10.2	15	25.4	2	3.4	0	0.0	59
5× 1	68	60.7	4	3.6	28	25.0	6	5.4	6	5.4	112
24×32	28	47.5	10	16.9	15	25.4	6	10.2	0	0.0	59
Totals	252	62.7	33	8.2	96	23.9	14	3.5	7	1.7	402

Total pendent 70.9% Total erect 27.4% Intermediate 1.7%

are noteworthy. There are a few plants, 1.7% in all, in which the fruit position is neither pendent nor erect but essentially intermediate. Most of the others are entirely of one type or the other, although in some cases (11.7%) both pendent and erect fruits occur on the same plant. Such exceptions have been observed from time to time in the field and in the greenhouse (fig. 6) and have been reported by previous investigators. Their occurrence indicates that the genetic mechanism controlling fruit position is subject to occasional modification, presumably by physiological factors.

The segregations from crosses in which the female parent was pendent conform very well to the simple monohybrid ratio but those from the reciprocal crosses (5×1 and 24×32) show significant departures from the expected 3:1 ratio. Several possible explanations of this exceptional behavior suggest themselves: 1. It may be a chance difference due to unrepresentative sampling; but in the most extreme case (24×32) the deviation from expectancy is so wide that a greater one would be expected only about twice in a hundred times. 2. There may be a maternal influence on the fruit position, since segregates from crosses in which the seed parent was erect show a much higher proportion of erect types than those in which the pollen parent was erect. This explanation is improbable since there is no visible difference in fruit position among F_1 plants from these reciprocal crosses. 3. Certain lines (1 and 32) may influence the segregation through the possession of factors modifying the expression of dominance, as suggested by Fisher (1931). It is conceivable that such factors, in their assortment with the primary pendent-erect gene, might tend to neutralize the effect of this gene to a varying degree. This hypothesis also serves to explain the somewhat conflicting data presented by the previous and present investigators of the problem. The intermediate position of the fruits in

the F_1 of some crosses (not observed by the writer), for example, might be the result of such modifying factors present in the lines used. Such an explanation does not readily lend itself to experimental verification, although data from additional crosses involving those lines suspected of possessing modifying factors might contribute confirmatory evidence.

In general, the exceptions found in the present work are relatively few in number and the writer feels that their occurrence does not invalidate the main conclusion that a single gene difference is essentially responsible for the opposite fruit positions found in pendent and erect plants.

GEOTROPIC RESPONSE

The question presents itself as to whether or not the position of the fruit is the expression of a growth response to gravity. It seems to be more definitely related to the force of gravity than to the polarity of the axis (fig. 1). To test this, clinostat experiments were attempted but proved unsuccessful because of technical difficulties. The following experiment was then performed. Genetically pendent and genetically erect plants were placed on their sides while yet young and permitted to continue their development; control plants of the same genetic constitutions were grown in their normal position. After a time the laterally placed plants showed, in addition to the expected change in position of the leaves and young stems, a marked change in fruit position. In the erect plants the fruit stalks assumed a vertical position in their development causing the stigmatic ends of the fruits to point straight up (fig. 4). In the pendent plants the fruit stalks curved so that the mature fruits pointed downward. In each case the fruits were nearly perpendicular to those of the control plants when the two were compared in the same position (fig. 5).

Some of the experimental plants were placed on their sides after one or more of their fruits had set, in order to determine the threshold of sensitivity of this geotropic response. It was found that the fruits would show the characteristic response up to about one-third of their maximum size, an incomplete response until they were about two-thirds grown, and no response after that. The bending is evidently not due merely to the weight of the fruit, as some of the previous investigators have suggested, but is a true growth movement. This was confirmed by microscopic examination of the curved fruit stalks which showed that the cells on the convex side were considerably longer (and larger) than those on the concave side.

Several young fruits from whose stigmatic ends about 1 mm. had been removed were tested for the geotropic response exhibited by the normal fruits. Positive results were obtained in all cases, indicating that it is not the extreme tip of the organ which is sensitive to gravity.

DISCUSSION

The chief interest of this study lies in its demonstration of the specific effect shown by a gene on a growth response. Comparatively few cases of single gene differences responsible for such physiological characters have been reported. The inheritance of a tactic response in *Drosophila melanogaster* has been studied by McEwen (1918). He found that, "in a mutant stock of flies known as tan, there is clear-cut evidence for the sex-linked inheritance of a character which may be described as indifference to light. It is apparently not due to any structural defect in the eye." These tan flies thus fail to exhibit the positive phototaxis characteristic of the wild type. The writer has found no previous mention in the literature of the inheritance of a geotropic response with the exception of a footnote in Ikeno's paper which indicates that an acute bending of the flower stalk in erect-fruited peppers (figs. 2, 4) does not appear when the plants are rotated horizontally about their long axes on a clinostat. Apparently the same (stalk) cells that show an unequal growth with respect to the force of gravity in the development of the fruit, exhibit a similar type of response in the opening of the flower bud, and it seems probable that the same gene determines the sensitivity in both cases.

The mechanism by which this gene regulates the sensitivity of the stalk cells to gravity is as yet unknown. The results of studies on the geotropism of root and stem tips, however, are very suggestive. The unequal growth which results in the bending of these organs has been claimed by Cholodny (1929) and others to be due to the localization of a growth-regulating substance (or substances) as a result of the one-sided stimulation. This substance, whether extracted from root tips or coleoptiles, retards the growth of root cells and accelerates the growth of shoot cells (Keeble, Nelson and Snow 1931). Thus, the same material evidently calls forth the opposite geotropic responses of root and stem. This difference in geotropism between root and shoot, which appears as the result of differentiation, may perhaps be similar to that between pendent-fruited and erect-fruited types of pepper plants, which is evidently due to a gene difference. If the cause of the former difference were understood, it would provide a clue as to that of the latter, for how a gene operates in producing differences in growth response to gravity is a question which as yet remains unsolved.

SUMMARY

1. Pendent fruit is dominant over erect fruit in the F_1; the generally monofactorial segregation in the F_2 indicates that a single gene difference is involved.

2. The hypothesis of factors modifying the expression of dominance is applied to certain exceptional segregations.

3. Experiments indicate that the position of the fruit is an expression of the genetically determined growth response of the stalk with respect to gravity.

4. The resemblance between this genetico-physiological interaction and the differential growth responses exhibited in the familiar bendings of root and stem is discussed.

The writer wishes to acknowledge his gratitude to Mr. Morton Goldstein and to Mr. Louis Jaffe for their assistance in recording much of the data. To Prof. E. W. Sinnott of Barnard College, Columbia University, he is particuarly indebted for material and greenhouse facilities and for helpful suggestions and criticism.

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Explanation of Plate 6

Fig. 1. Pendent plant of line 8. (9-inch pot)
Note almost horizontal branch to the left bearing fruits at right angles to it.

Fig. 2. Erect plant of line 24. (9-inch pot)

Fig. 3. F_1 plant of 8×24. (9-inch pot)
The dominance of the pendent type is shown.

Fig. 4. Erect plant with fruit showing negative geotropism. (4-inch pot)

Fig. 5. Pendent plants with fruits showing positive geotropism. (4-inch pots)
The plant at the left was grown in a horizontal position.

Fig. 6. Exceptional plant showing various fruit positions on the same individual. (9-inch pot)

The nutritional requirements of the fungus, Aspergillus niger

ROBERT A. STEINBERG

Formulae for nutrient solutions supposedly containing all essential ingredients in amount just sufficient for maximum normal growth of *Aspergillus niger* have been proposed from time to time. While there has been general agreement concerning the well known nutrients, agreement as concerns the proportions in which they are required is lacking and controversy with respect to any heavy metals that may be necessary has been continuous. Though growth increases have been reported with many of the chemical elements assumedly as a consequence of chemical stimulation through toxicity, these increases have failed of confirmation or acceptance by others. The hypothesis of "chemical stimulation," or increase in mass through toxicity suggested originally by Pfeffer to elucidate the behavior of *A. niger* with zinc, has proved indeed a serious obstacle to progress in this and analogous fields, inasmuch as it afforded an all too ready, if erroneous, explanation for data based upon an inadequate technic (Steinberg 1932, 1934). It is only in comparatively recent times and through the work of the author (1919, 1920), Bortels (1927, 1928) and Roberg (1928, 1931) that the necessity for iron, zinc and copper was definitely ascertained. The statement by the author (1934) that manganese is also necessary and that iron, zinc, copper and manganese cannot replace each other or be replaced by other elements in the metabolism of the fungus is based in part on the data in this paper.

The methods employed in carrying out the investigations here reported upon are identical in the main with those described in previous publications by the author. The same "W" strain of *A. niger* was used throughout through the courtesy of Dr. Charles Thom in whose laboratory this strain has been maintained since 1917. It may be mentioned in passing that the fungus has seemed to have undergone no change in appearance or behavior to zinc (optimum 0.1 mg./L) during this interim. The cultures, however, were grown in 200 cc. pyrex Erlenmeyer flasks at 34.7–35.0°C. for six days, instead of in 150 cc. flasks at 30–31°C. for seven days. The bread cultures for inoculation of the flasks were dispensed with and a spore suspension used. The inoculation dosage was approximately 0.05 mg. dry weight of spore material per flask. The flasks, each containing 50 cc. of nutrient solution, were sterilized in the Arnold sterilizer by steaming for ten minutes. Where autoclaving is indicated as in nutrient solution purification, it was for 20 minutes at a pressure of one atmosphere (15 lbs.). Acidity readings were obtained with a Leeds and Northrup poten-

tiometer using a quinhydrone electrode—galvanometer deflections being read with a microscope magnifying sixty diameters. The pH values are assumed to be accurate to 0.01 pH.

The formulae for several nutrient solutions are given in table 1. The solutions included are the Raulin, the Pfeffer and a number particularly studied by the author for purposes of comparison. The composition of the Raulin solution has been omitted since it is quite complex and has been printed repeatedly. The values for the heavy metal salts recommended have also been omitted since they are given in table 2. The total concentration of inorganic salts per liter of the author's dibasic solution, it is important to note, is less than half that of the Raulin optimum solution, and but little more than one-sixth that of the Pfeffer optimum solution.

TABLE 1

Solutions for optimum growth and development of A. niger

	RAULIN	PFEFFER	MONOBASIC	(RAULIN)	DIBASIC	TRIBASIC
Water	1000.0 g	1000.0 g	1000.0 g	1000.0 g	1000.0 g	1000.0 g
Sucrose	46.7	50.0	50.0	50.0	50.0	50.0
NH_4NO_3		10.0	2.0	3.0	2.0	2.0
KH_2PO_4		5.0	0.75	—	—	—
K_2HPO_4		—	—	0.6	0.48	—
K_3PO_4		—	—	—	—	0.39
$MgSO_4 \cdot 7H_2O$		2.5	0.6	0.67	0.6	0.6
Total Salts	6.71	17.5	3.35	4.27	3.08	2.99
Approx. pH		4.25	4.66	7.06	7.13	7.86
Max. yield		1022.1	1010.6	1051.1	1083.3	(1010.2)

The number of milligrams per liter of the elements contained in these solutions is given in table 2. The dibasic solution labelled as (Raulin) is quite similar in composition to the real Raulin solution, excepting for the heavy metals, and far simpler to prepare. The amounts of iron, zinc, copper and manganese required in the Pfeffer solution were determined to be 0.05, 0.10, 0.02 and 0.01 mg. per liter respectively with the particular lot of chemicals employed. The absolute optima should include the amounts of heavy metals added as impurities with the nutrients used.

The new solutions presume the use of commercial chemicals of maximum purity, sucrose containing not over 0.0025 per cent ash and water redistilled in pyrex glass. None of these materials, there is reason to believe, are absolutely free from the heavy metals required by the fungus, and the amounts of these impurities vary with the lot of chemicals. The redistilled water used without doubt also contained contaminants. According to Cliquet, Guilbert and Rénau (1933) water so prepared still con-

TABLE 2

Milligrams per liter of the elements (exclusive of carbon, hydrogen, oxygen) contained in the solutions of table 1

	RAULIN	PFEFFER	MONOBASIC	(RAULIN)	DIBASIC	TRIBASIC
N	1017.0	3500.0	700.0	1050.0	700.0	700.0
K	250.0	1435.0	215.3	269.4	215.5	215.5
P	108.0	1140.0	171.0	106.8	85.4	56.9
Mg	66.0	247.5	59.4	66.0	59.4	59.4
S	53.0	325.0	78.0	86.7	78.0	78.0
Fe	9.4	tr.	0.125	0.075	0.125	(0.25)
Zn	10.6	—	0.16	0.10	0.14	(0.18)
Cu	—	—	0.02	0.01	0.02	(0.06)
Mn	—	—	0.01	0.01	0.01	(0.06)

tains 5 mg./L of solids, including 0.05 mg. lead, 0.05 mg. copper and 0.02 mg. boron. The heavy metals are added as sulphates.

The necessity for the heavy metals included in the formulae is brought out in table 3. The growth ratio values in these tables represent the quotient of the yield in the presence of an element divided by the yield in its absence. Special attention is called to the data on manganese. Despite repeated assertions to the effect that this element is not essential for *A. niger*, Bertrand and Javillier (1911) have claimed it is necessary both for the growth and sporulation of this fungus. More recently Bortels (1927) and Roberg (1928) also state that manganese is not required by this fungus. The evidence given by the yields, sporulation, acid production and non-replaceability in the tables of this paper substantiates the view of Bertrand and Javillier.

The tribasic solution is not quite optimum for growth, being deficient in phosphate. While not actually checked there is sufficient evidence to warrant the statement that only the addition of 30 mg. P (one drop H_3PO_4) per liter is needed to obtain maximum yields. The maximum yield noted for this solution in table 1 is considered excessive and due to accidental inclusion of an increased amount of the precipitate that forms in this solution when mixed.

Supplementary evidence for the necessity of the heavy metals is also afforded by variations in acidity encountered in the cultures. These have been summarized in table 4.

The final acidity would seem to depend upon the initial acidity of the nutrient solution only in minor degree. Acidity at harvest is greatest almost invariably in the cultures from which manganese has been omitted. Then follow the full nutrient cultures, the minus copper, the minus iron, and the minus zinc or minus heavy metal in the order given. Increases in

TABLE 3

Effect upon growth of the omission of heavy metals from the nutrient solution

HEAVY METAL OMITTED	YIELDS (MILLIGRAMS DRY-WEIGHT)				
	PFEFFER	MONOBASIC	(RAULIN)	DIBASIC	TRIBASIC
All	213.8	72.4	156.7	80.7	48.8
Fe	842.8	322.6	422.1	340.5	175.6
Zn	147.0	76.5	121.9	111.5	62.7
Cu	903.9	928.6	928.9	959.9	880.3
Mn	696.5	402.0	742.7	821.0	428.0
None	1012.5	1003.3	1047.9	1061.2	947.6

HEAVY METAL	GROWTH RATIOS				
	PFEFFER	MONOBASIC	(RAULIN)	DIBASIC	TRIBASIC
All	4.74	13.86	6.69	13.15	19.42
Fe	1.20	3.11	2.48	3.12	5.40
Zn	6.89	13.12	8.60	9.52	15.11
Cu	1.12	1.08	1.13	1.11	1.08
Mn	1.45	2.47	1.41	1.29	2.21

acidity of the cultures follow in the same order. Conditions favoring the production of organic acids would seem to include the use of low initial acidity, the presence of iron, zinc and copper, and the omission of man-

TABLE 4

Effect upon acidity (pH) of the omission of heavy metals from the nutrient solution

HEAVY METAL OMITTED	pH AT HARVEST				
	PFEFFER	MONOBASIC	(RAULIN)	DIBASIC	TRIBASIC
All	2.40	2.78	2.41	2.48	2.37
Fe	1.74	1.99	1.71	1.89	2.16
Zn	2.49	2.48	2.38	2.34	2.63
Cu	1.68	2.14	1.67	2.44	2.36
Mn	1.68	1.91	1.50	1.94	1.58
None	1.64	2.11	1.64	2.48	1.92
Initial	4.25	4.66	7.06	7.13	7.86

HEAVY METAL OMITTED	DECREASE IN pH DURING GROWTH PERIOD				
	PFEFFER	MONOBASIC	(RAULIN)	DIBASIC	TRIBASIC
All	1.85	1.88	4.65	4.65	5.49
Fe	2.51	2.67	5.35	5.24	5.70
Zn	1.76	2.18	4.68	4.79	5.23
Cu	2.57	2.52	5.39	4.69	5.50
Mn	2.57	2.75	5.56	5.19	6.28
None	2.61	2.55	5.42	4.65	5.94

ganese. The observation by Currie (1917) that citric acid production is greatest when the dry-weights formed in the cultures are small and the felts are sterile and curdy in appearance does not coincide exactly with the aspect and final pH of the minus manganese culture.

Additional evidence bearing on the necessity of iron, zinc, copper and manganese in the metabolism of the fungus is afforded by experiments in which attempts are made to replace any one of these elements. Including these four heavy metals a total of seventeen chemical elements were studied.

The experiments were of two kinds (table 5). In one series an attempt was made to substitute iron, zinc, copper or manganese for each other (double doses) or by each of the other elements dealt with. The effects upon growth are stated in the form of growth ratios. In the other series (last row) an attempt was made to increase growth in the full nutrient solution containing iron, zinc, copper and manganese through addition of each of the other elements. The salts of the elements utilized were the sulphates, excepting for $HgCl_2$, $KF \cdot 2H_2O$, As_2O_3, H_3BO_4, $CoCl_2 \cdot 6H_2O$ $UO_2(NO_3) \cdot 6H_2O$, $Na_2SiO_3(9H_2O?)$ and $(NH_4)_6Mo_7O_{24} \cdot 4H_2O$. All were added at a concentration of 1 mg./L, excepting mercury and beryllium which were used at 0.10 mg./L.

The data in table 5 indicate that iron, zinc, copper and manganese cannot be replaced by each other in the metabolism of the organism or by any of the other chemical elements investigated. Since iron, zinc, copper and manganese were employed at a concentration of 0.20, 0.14, 0.06 and 0.04 mg./L, respectively, the majority of these so called "stimulants" gave no evidence of "stimulation" or of substitution at concentrations five to twenty-five times that of the four essential heavy metals. Thallium at 1 mg./L was also without effect upon growth when added to the complete nutrient solution as sulphate, the growth ratio being 0.94. The only effects of toxicity to be detected were inhibition or suppression of spore formation or a decrease in yield.

Exception to the above statements possibly should be taken with respect to the data with cadmium and zinc, and fluorine and zinc. Since the first named element gave the largest growth increase when substituted for zinc, additional work was performed with this element. Whereas it would be improbable that samples of the purest commercial $3CdSO_4 \cdot 8H_2O$ obtained from different manufacturers would contain exactly the same amount of zinc as impurity, while the cadmium content of the different cultures could be made almost identical, an experiment was carried out with four different samples of this salt. The first was of domestic origin and

TABLE 5

The growth ratios obtained with various chemical elements in a purified solution when substituted for iron, zinc, copper or manganese, or when added to the complete nutrient solution

ELEMENT OMITTED	CONTROL		GROWTH RATIOS																
			DOUBLE DOSE*				1 mg./L**												
	GROWTH RATIO WITH OMITTED ELEMENT	VARIATION IN GROWTH RATIO WITH THE ELEMENT OMITTED	Fe	Zn	Cu	Mn	Co	Ni	Cd	Hg	U	Mo	Al	Be	Li	As	B	F	Si
Fe	55.43	0.84–1.20	—	0.72	0.97	0.70	1.93	1.57	0.70	1.25	0.81	0.89	1.00	0.75	0.82	0.84	1.07	2.14	0.91
Zn	5.08	0.84–1.19	0.60	—	0.85	1.45	1.78	1.29	3.81	0.41	1.24	0.70	0.75	0.60	1.15	0.65	1.16	0.80	0.69
Cu	1.61	0.99–1.02	0.88	0.94	—	0.91	1.00	0.91	0.91	0.86	0.87	1.03	0.97	0.98	0.93	1.07	0.95	0.81	0.92
Mn	1.51	0.99–1.01	1.11	1.10	0.94	—	1.04	0.98	0.78	0.95	1.00	1.21	1.00	0.98	0.94	0.98	0.95	0.94	1.02
Zn	69.34	0.49–2.02	1.04	—	1.01	1.01	—	1.05	3.74	0.97	—	—	—	1.07	1.47	—	—	2.00	—
Cu	2.06	0.67–1.49	1.13	1.32	—	1.10	—	1.12	1.20	—	—	—	—	1.06	1.17	—	—	0.93	—
Mn	1.21	0.83–1.20	0.97	1.11	0.99	—	—	0.83	0.99	—	—	—	—	0.95	1.07	—	—	0.94	—
—	—	0.87–1.15	0.94	1.18	0.95	0.97	0.96	0.86	0.86	1.06	1.06	1.00	1.07	1.03	1.04	1.10	0.98	1.08	1.04

* Respectively 0.40, 0.28, 0.12 and 0.08 mg./L; and last row 0.25, 0.18, 0.04, 0.02.

** Except mercury and beryllium at 0.1 mg./L.

labelled as containing not over 0.05 per cent zinc, the second was the same material specially twice recrystallized by the manufacturer, and the third was the first sample partially precipitated as phosphate and filtered. The last sample was of foreign origin and made no specific claim as to freedom from zinc, but the claims made with respect to other impurities would give the impression that the salt was of exceptional purity. Table 6 summarizes the data obtained with these four samples by substituting 1 mgCd/L for less than 0.2 mgZn/L.

TABLE 6

The effect of different samples of 3 $CdSO_4 \cdot 8\ H_2O$ upon the growth of A. niger in a zinc-free but otherwise complete nutrient solution

HEAVY METAL ADDED	INITIAL pH=6.37		INITIAL pH=7.80	
	YIELD	GROWTH RATIO	YIELD	GROWTH RATIO
—	42.5 mg.	—	27.8 mg.	—
Zn	923.9	21.74	945.4	34.01
Cd (No. 1)	250.8	5.90	49.6	1.78
Cd (No. 2, special)	226.1	5.32	67.7	2.44
Cd (No. 3, purified)	268.7	6.32	76.9	2.77
Cd (No. 4)	364.0	8.56	77.8	2.80

Not only do the different lots of cadmium salt have far smaller effects upon growth than does zinc, but their effects it will be noticed differ among themselves. Since great care was exercised in the preparation and addition of these various samples, the differences in response, and probably the response itself, cannot be ascribed to the cadmium ion but should more properly be attributed to a variation in amount of zinc impurity present in the various samples. The difference in response in the two experiments would also tend to support this interpretation. Though removal of zinc is more complete in the solution at pH 7.80 (as shown by the lower yield on non-addition of zinc and the higher yield on its addition) the effect of the addition of cadmium was diminished.

Aside from the evidence furnished by the yields, omission of heavy metals from the purified solution is accompanied by characteristic and striking changes in appearance of the felts. Upon non-addition of either iron or zinc, no felts are formed but the translucent hyphae grow submerged in the solution and sporulation is practically suppressed. A minute amount of zinc, it must be emphasized, is essential for sporulation. Failure to add copper also results in a sharp diminution in sporulation and the spores that are formed are white, yellow or brown instead of the normal black. Omission of manganese, lastly, results in the development of intense white felts consisting of individual and but partially coalesced

colonies. The brittle felt is, as a result, perforated by numerous holes. Spore formation, moreover, is sharply reduced or even suppressed in the absence of manganese.

The morphological response to heavy metal deficiency varies also with the specific element. The first sign of an iron or zinc deficiency is usually a decrease in yield, accompanied perhaps by an apparent increase in sporulation if the complete nutrient is not optimum, and only when the deficiency is almost complete does sporulation become markedly inhibited. With copper in insufficient amount, on the other hand, sporulation is affected even though the yield is practically undiminished. Suppression of spore formation in cultures containing a limited amount of manganese has been noted at yields three-quarter maximum.

While it has been possible to bring about marked increases in growth ratios with the heavy metals by use of minimum quantities of nutrient solution components, the results achieved do not equal those obtained with the method of nutrient solution purification excepting with manganese. Nevertheless the data obtained are of value if only to show the importance of the impurities present in the ingredients of the nutrient solution, and as an indication of the proportions of these ingredients required for maximum normal growth.

The greater dilution of the new solutions that were found capable of bringing about maximum production of mass would seem to be dependent upon the inclusion of iron, zinc, copper and manganese in their composition. Intentional omission of an essential element from the nutrient solution must, if maximum growth is attained, be compensated by its unintentional addition as an impurity in the compounds that are added. The result is the addition of a nutrient to excess in order to have sufficient of its accompanying impurity to meet the requirements of the fungus. This is illustrated by a comparison of the zinc optima for the Pfeffer and the mono-basic solutions. Computed from values specially determined by the manufacturer for the salts used, the amount of zinc impurity added to the former with the salts is 0.07 mg/L and to the latter 0.01 mg/L. The optima, as determined experimentally are 0.10 and 0.16 mg/L, respectively. The total amount of zinc required for maximum growth is then actually the same in each solution, or 0.17 mg/L. Similar values might also be computed for the other elements in an analogous manner. The concentration, it might also be noted, of a nutrient solution containing all essential components in optimum amount is the minimum total concentration capable of resulting in maximum growth.

That the formulae contain all the elements essential for the growth

of *A. niger* is improbable. An improvement in technic or even the use of a lot of chemicals of accidentally greater purity may lead to the discovery of additional necessary components. On the other hand, of the twelve elements found to be essential for this fungus all but copper have been claimed to be essential for the higher plant, and all but zinc in the nutrition of the animal. These experiments, moreover, tell us little respecting those elements (sodium, aluminum, boron, arsenic, silicon) present in the glassware used.

The experimental results would appear to justify the following conclusions. 1. The optimum nutrient solution (containing five per cent sucrose) for maximum normal development of *A. niger* has a total salt concentration of about 3.0 grams per liter. 2 Iron, zinc, copper and manganese are essential for the normal growth and sporulation of this fungus. 3. Use, as in the Raulin and Pfeffer optimum solutions, of excessive amounts of nutrients containing traces of other essential constituents may mask the necessity for these other components. 4. Toxicity, whether sporulation is or is not inhibited, does not lead to an increase in mass. 5. At the concentrations employed, zinc and iron are required for acid production, manganese is unnecessary and prevents the attainment of maximum values, while copper aids the process of acid formation but slightly.

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Embryo sac development and cleistogamy in Commelinantia Pringlei

MABEL PARKS

(WITH PLATES 7 AND 8)

Commelinantia Pringlei (S. Wats.) Tharp, originally was given the name *Tradescantia Pringlei* by S. Watson from material collected near Monterrey, Mexico. Correspondence with Dr. F. W. Pennell who had access to herbarium material had led Dr. B. C. Tharp (1922) to suspect that it was not a *Tradescantia* but that it belonged to his new genus *Commelinantia* which he established as a result of the study of *Tinantia anomala* C. B. Clark, originally described by Torrey and assigned by him to the genus *Tradescantia* as *T. anomala*.

Dr. Tharp collected abundant material of the plant in the vicinity of Monterrey in 1923. Examination of this fresh material confirmed his suspicions as to its relationship to *Commelinantia* and in 1927 he transferred it to this genus.

In his study of *C. Pringlei* Tharp (1922) found that it bore cleistogamous flowers on its lower branches and normal chasmogamous flowers on the upper branches. He says:

"Cleistogamous flowers occur on the lower portions of the stems both above and below the soil surface, appearing in general before the aerial ones, usually singly disposed at the ends of positively geotropic capillary branches, each of which bears one to three such reduced leaves (usually only sheaths 5–6 mm. long) below the flower; sepals similar to above (chasmogamous forms) except less hooded, smaller and decidedly purplish throughout; petals also similar except progressively smaller downward on the stem, those below the soil surface much reduced; stamens slenderer, less hairy, and with anthers much reduced; ovary and stigma similar but with a shorter style; ovules two in each cavity, superimposed; seeds similar to those of *C. anomala* in that the endosperm is separated on one side by a suture which extends to the embryo-cavity; but the seeds from cleistogamous flowers are much rougher, with scalloped, shelving, lateral ridges, and are larger."

The use of the term "cleistogamy" began with Kuhn (1867) who described the closed flowers of *Vandellia sessifolia* Benth., first referring to them as "sogenannte monoicodimorphic Blüthen," a term which he ascribes to Darwin. He objects to the application of this term to flowers of this type. He says "Was die Namen monoicodimorph und Monoicodimorphismus anbetrifft, so erscheint er . . . bei dem wachsenden Materiale

für viele Falle so unzweckmässig, dass ich statt dessen den zutreffenden Namen—*Cleistogamismus* und flores *cleistogami* vorschlagen möchte." The term cleistogamy still conveys a somewhat generalized idea of a permanently closed flower. The degree of development of such closed flowers varies considerably as is well seen in *Commelinantia Pringlei.* While some speak of all of the closed flowers, whether above or below ground as cleistogamous, as Dr. Tharp in referring to *Commelinantia*, others, as Bergdolt (1932), speak of the more conspicuous aerial closed flowers as "Uebergangstadien." Miss West (1930) calls such flowers "semicleistogamous." Hansgirg (1893) uses the term "pseudo-kleistogam" to characterize flowers which are normally chasmogamous, but are prevented from opening by unfavorable external conditions such as rain or cold and, as a result, become self pollinated. On the other hand Kirchner, Loew, and Schroeter (1908) regard the more conspicuous aerial closed flowers of whatever origin, as "pseudokleistogam."

The term "chasmogamy" proposed in 1869 by Axell to characterize flowers which normally open has some of the ambiguity of "cleistogamous" in that some writers include under it some of the transitional forms.

Von Mohl (1863) has called attention to the occurrence of open and closed flowers on *Commelina benghalensis* L., giving credit to Weinmann (Regenb. Flora, 1920, p. 733) for the first description of the phenomenon in this plant. Reference is also made to Wight's excellent illustration of the plant, showing the two kinds of flowers (Icon. pl. Ind. orient. VI. Tab. 2065). This illustration has been reproduced in Engler and Prantl's Natürlichen Pflanzenfamilien (1889).

Knuth (1906) lists *Tradescantia erecta* Jacq. as a form in which cleistogamy occurs but makes no reference as to his authority. It is of interest to note that *T. erecta* is a synonym for *Tinantia fugax* Scheidm. These two examples of cleistogamy together with the case of *Commelinantia Pringlei* (S. Wats.) Tharp seem to be all so far reported for the Commelinanceae.

The material used in this study was grown in the university greenhouse and in the garden of Dr. F. McAllister. The original plants were brought to Austin from Monterrey, Mexico, in 1923 by Dr. B. C. Tharp.

The collections of this material were made from September 1932 until March 1933. During the fall the collections were made from the garden. When the weather became too cold the plants were placed in the greenhouse. Those plants kept in the greenhouse bore both normal and cleistogamous flowers profusely during the winter months.

The plants were taken out of the ground and washed carefully. The

cleistogamous flowers were removed and fixed in Merkel's or strong chrom-acetic fixatives. Both gave equally good results.

The buds were cut from five to seven microns thick. The seeds have very hard coats and only celloidin imbedding gave satisfactory results. These sections were cut about sixty microns thick. The sections intended for gross study were stained in Delafield's haematoxylin and those intended for cytological study were stained in Heidenhain's iron-alum haematoxylin.

GROSS STRUCTURE OF THE CHASMOGAMOUS AND CLEISTOGAMOUS FLOWERS

The chasmogamous flowers found on the upper branches produce three equal sepals of pale green, with purple margins and three equal lavender petals 6–8 mm. long by 8–10 mm. wide. Notwithstanding the fact of equal sepals and petals, the flower is definitely bisymmetrical as is shown by the differentiation of stamens. Since the distribution of the stamens is similar to that in *C. anomala* which has a definite anterior-posterior arrangement of petals, the same terminology as used in the description of *C. anomala* is followed here. The stamens are of four types. The posterior has a ring of yellow hairs slightly below the middle, and the filament is divided into a yellow upper and a blue lower portion. The two postero-lateral stamens are slightly larger than the posterior, and the ring of hairs is higher on the filament. These three stamens have yellow anthers. The anterior-lateral stamens are long and slender with a ring of blue hairs below the middle. The anterior stamen has no hairs and is slightly larger than the rest. The ovary is terminated by a long curved style and a yellow stigma. The size range of the floral envelope is quite marked, apparently much influenced by humidity and soil water.

The chasmogamous forms appearing on the small branches just above the soil surface have sepals similar to those flowers in the apical region and decidedly purple. The petals, which are similar in color to those of the apical chasmogamous form, are much reduced, but the size varies in the individual flowers. The stamens and pistil appear to be the same as those produced in the upper portion of the plant.

The cleistogamous forms are produced, and mature their seeds below the surface of the ground. In the mature stages of the flower the external appearance is that of a flower bud. This bud and the branch on which it is borne are tinged with lavender. The bud is at first enclosed by three bracts which also have this lavender tint. Although the flower elongates as it develops, there is little change in the diameter until after the pollen is fully mature. The flowers shown in figures 8 to 11, plate 7, all have the same

approximate diameter, although they represent stages from the beginning of the anthers to mature pollen.

In the material used for this study, the author has found no flowers above the surface of the ground that were clearly cleistogamous. Small flowers were common on the lower parts of the stem, but all which were above the ground showed at least a partial opening of the corolla. The petals were much smaller than those of the upper chasmogamous flowers, but distinctly violet in color. They are similar in size and general appearance to cleistogamous flowers which were induced to open by uncovering.

MORPHOLOGY OF THE CLEISTOGAMOUS FLOWER

At first the cleistogamous flower is a rounded mass of undifferentiated tissue covered over by a protective bract and two sheathing bracts. Soon the sepals arise as lateral projections. As they grow upward they bend inward and form an arched enclosure in which the other flower parts arise. The stamens arise next before the enclosure is completely formed. At this stage the outer bracts begin to wither. Before the stamens have become very much enlarged the petals begin to develop, followed closely by the carpels (pl. 7, figs. 5, 6, 7, 8). During the period of the development of these parts the pedicel elongates pushing the bud out of the withering bracts. The three carpels undergo an incomplete fusion to produce a pistil with a hollow style (pl. 7, fig. 9). At the time of fusion the stamens are bent toward the center and the anthers have begun to differentiate. The very young ovary is approximately spherical in shape. The ovules of each cavity first lie in the same horizontal plane. When first differentiated the ovules are almost orthotropous, but they soon become bent in a horizontal plane so that the micropyle is approximately at right angles to the point of attachment thus producing a campylotropous condition with the micropylar region on opposite sides of the ovarial cavity. In the nearly spherical ovary the ovules lie back to back. As the ovary elongates they come to lie one above the other.

While the carpels are still incompletely fused, the pollen mother cells are already in the prophases of the reduction division, and when the style is only partially developed, the pollen is mature (pl. 7, figs. 9, 10, 11). The style elongates, and soon a glandular stigma is formed in contact with the anthers. This occurs at about the time the outer and inner integuments of the ovules are recognizable and the megaspore mother cell is preparing for division (pl. 7, fig. 12). At about this time the outer bract can no longer be identified and the protective inner bract has begun to disappear. Due to the crowded conditions, caused by its tightly sheathing floral parts, the elongation of the ovary causes the style to become crumpled and the

stigma to be pressed close to the anthers (pl. 7, fig. 14). The pollen germinates at this stage and the tube makes its way to the glandular stigma (pl. 7, fig. 16). Somewhat later the bracts have disappeared and the petals and sepals are degenerating rapidly (pl. 7, fig. 15). The ovary becomes still further enlarged forcing its way out of the degenerating parts with the withered style and stigma still remaining attached (pl. 7, fig. 17).

There are two ovules in each of the three cavities not all of which mature. This elimination of ovules frequently occurs even before the time of fertilization as many of the ovules begin to degenerate at the time of the two-nucleate embryo-sac. Often there will be two seeds in one cavity and none in the rest, thus causing the capsule to be bent and distorted. The mature capsule dehisces in the same manner as those formed by the chasmogamous flowers. Although the flowers differ in size in the later stages, the order of the appearance of flower parts in the cleistogamous and chasmogamous flowers is the same.

DEVELOPMENT OF THE FEMALE GAMETOPHYTE

Guignard (1882) shows in *Commelina stricta* in an early stage a large axial subepidermal cell with a large nucleus and numerous granulations in the cytoplasm. The cell divides unequally. Of the resulting cells the micropylar is about one-third the size of the chalazal. The inner daughter cell crushes the outer one which becomes a conspicuous refractive band. Guignard interprets this disintegration of the outer cell as proving that the axial subepidermal cell is the mother cell. Consequently the crushed cell is not the "calotte," formed from the parietal cell. According to this interpretation, the embryo-sac arises from the inner cell of the first division of the megaspore mother cell. It follows that the two nuclei, which are potentially megaspore nuclei, enter into the formation of the embryo-sac. This is the so-called *Scilla* type of Ishikawa (1918).

Strasburger (1879) makes a bare reference to the unequal division of the megaspore mother cell in *Tradescantia virginica* which gives rise to a small upper and a large lower cell.

In *Commelinantia Pringlei* the megaspore mother cell is indistinguishable in size and content from the other cells of the nucellus until it enters into the prophases of the heterotypic division. At this stage the rapid enlargement of the cell and its nucleus, as well as the formation of the synaptic knot make it easily recognizable. In all cases there is a parietal layer lying between the mother cell and the epidermis.

After the first division of the megaspore mother cell the outer of the two resulting cells fails to divide (pl. 8, fig. 5). The outer of the two cells formed from the division of the inner daughter cell makes no growth and

the inner becomes the functional megaspore. Thus we have from the reduction division in the megaspore two small outer cells and a large inner cell, the two inner being sister cells (pl. 8, fig. 6).

After the first division of the functional megaspore, one nucleus goes to each end of the sac. A second division follows forming a row of four nuclei. These nuclei migrate to the outer end of the sac. The two inner nuclei very soon are seen to be noticeably larger than the two outer. Somewhat later one of the large nuclei is seen near the center of the sac, and the second large nucleus is seen below two small ones in the micropylar region. No definite membranes could be identified around the three micropylar nuclei in any preparations examined, but it seems clear that the small nuclei are nuclei of undifferentiated synergid cells and the large one that of the egg. The centrally located nucleus must be the only polar nucleus.

SEED FORMATION

During the development of the embryo-sac the outer integument undergoes thickening slightly below the base of the sac, forming a thick crescent shaped structure extending about three-quarters of the distance around the sporangium, being lacking only in the region of the funiculus. The cells of this constriction appear in section to be the same in structure as those of the rest of the integument, but they must form an unyielding crescent since no further enlargement in this region occurs. In the subsequent development very little swelling occurs on the micropylar side of the thickening. On the chalazal side of the thickening very rapid enlargement takes place so that very shortly the appearance is produced of a deep furrow-like constriction at the crescent shaped thickening of the integument. This is especially conspicuous as shown in longitudinal sections of the sporangium cut in a plane at right angles to the stalk. Evidence that this furrow is not due to growth inward at this region is seen in the constant thickness of the isthmus of tissue surrounded by the crescent.

By the time of fertilization that part of the sporangium on the chalazal side of the constriction is about three times as broad as that on the micropylar side of the constriction. This growth continues after fertilization, during the development of the endosperm and embryo.

The development of the embryo-sac and the early stages of endosperm development take place in that part of the megasporangium on the micropylar side of the constriction.

Only the very early stages of the development of endosperm have been observed and these show at least eight free nuclei. It is clear, therefore, that the endosperm development is the more common "nuclear" type, in

which many free nuclei are formed before they become separated by walls. The endosperm grows out through the isthmus and finally replaces all of the tissue on the chalazal side of the constriction which lies within the layer of sclerenchyma cells which seem to have been derived from the inner integument (text figs. 4–5).

The enlargement of this developing sporangium is at right angles to the

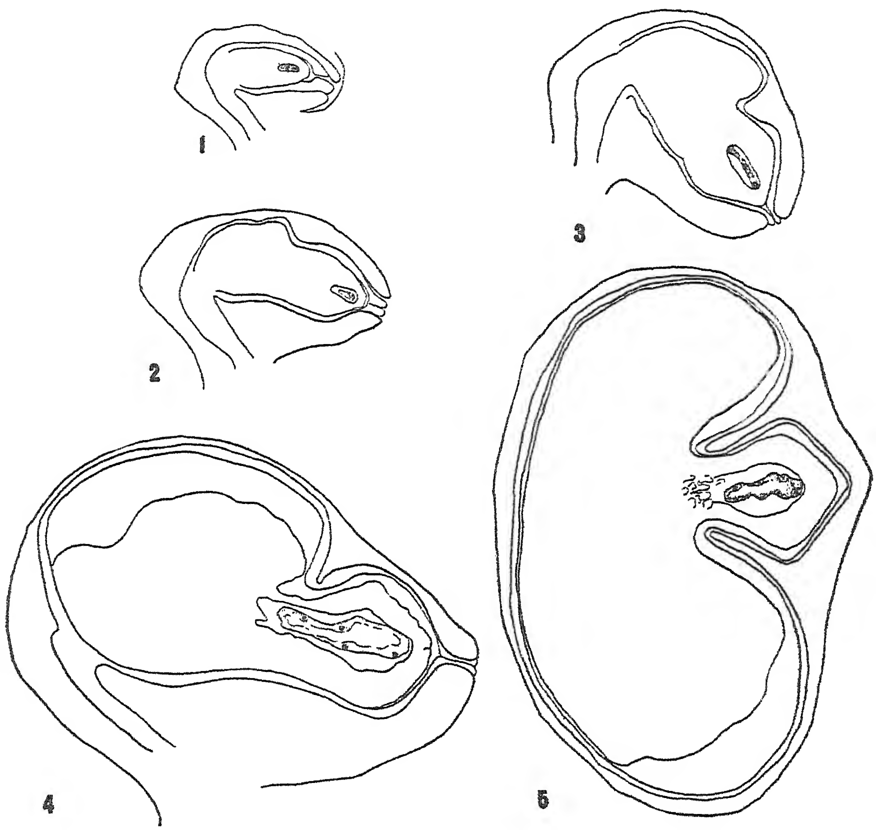

Fig. 1. The ovule at the time of megaspore formation. The integuments have surrounded the nucellar mass. ×24.

Fig. 2. The young ovule showing crescent shaped constriction in the outer integument. ×24.

Fig. 3. The basal portion of the sporangium is enlarged, and the furrow is stationary. ×24.

Fig. 4. The endosperm has begun to digest the nucellus and grow into the enlarged portion. ×24.

Fig. 5. Further enlargement of the basal portion. The crescent has not changed. The endosperm is being formed. ×24.

original long axis of the sporangium and in a plane at right angles to the stalk so that a much flattened seed results, having the shape of the bowl of a thick shallow spoon.

CLEISTOGAMY

In nature, the aerial flowers of *Commelinantia Pringlei* which appear at the base of the plant, produce an open blossom which may average about half the size of the typical chasmogamous form produced higher up. The petals are purple in color but much reduced. Those flowers which are produced below the ground also have rudimentary petals as may be seen in section (pl. 7, fig. 10). However, if these cleistogamous flowers are exposed to light, accidentally or otherwise, they produce small open flowers with purple petals.

The writer carefully removed the soil from several large plants. These plants were suspended in tall museum jars with their lower roots in water. Many of the cleistogamous flowers bloomed and the sheathing bracts turned green as is normal for chasmogamous flowers.

The stamens and pistils were mature before the flowers were exposed to light as is shown by the resemblance of these structures in the flowers which have been induced to open, to the same organs in the flowers which are still closed (as is seen in section). The petals are reduced in size and the margins are ragged due to the crowded conditions and the contact with the soil. The style does not have the graceful curve of the chasmogamous form, but is stubby and somewhat distorted. The stigma is slightly enlarged. All of the stamens are present, but some of the anthers have begun to wither.

Commelinantia anomala (Torr.) Tharp occurs commonly in the vicinity of Austin. Although it has the same interesting differentiation of the stamens as in *C. Pringlei*, it has two large, equal, "postero-lateral" petals and a rudimentary "anterior" petal. No cleistogamy has been observed in it.

The writer has examined sections of the flowers of *C. anomala* and finds the development of the embryo-sac essentially the same as in *C. Pringlei*. Two nuclei are noticeably larger than the others. A group of three nuclei composed of one large and two small nuclei, is formed in the micropylar end of the embryo-sac. No membranes were observed about these nuclei. The remaining large nucleus is the single polar nucleus.

A furrow-like constriction separates the micropylar part of the megasporangium, which contains the embryo-sac, from the much enlarged chalazal portion of the sporangium. The chalazal area becomes filled with endosperm upon the maturing of the seed while the embryo occupies the micropylar region.

From a superficial examination of the seeds of *Commelina* and *Tradescantia* it is clear that they are essentially the same as those of *Commelinantia*.

DISCUSSION

In *Commelinantia Pringlei* the megaspore mother cell is much larger than the neighboring cells and it is always accompanied by a parietal cell. Strasburger (1879) shows the presence of a parietal cell in *Tradescantia virginica.* Guignard's (1882) interpretation that in *Commelina stricta* the megaspore mother cell is sub-epidermal, has led him to the conclusion that the two inner megaspore nuclei enter into the structure of the eight-nucleate embryo-sac. This conclusion seems unjustified as nothing in his evidence shows that the embryo-sac is really sub-epidermal. From his figures it seems just as probable that the disintegrating cell, which he regards as arising from the first division of the mother cell, is the parietal cell. On the same plate Guignard shows these phenomena for *Commelina stricta*, also early disintegration of the parietal cell for other forms.

The inner of the two daughter cells from the second division becomes the functional megaspore. It divides twice to form a four-nucleate embryo-sac. This is the so-called Dicraea type of Ishikawa (1918). *C. Pringlei* follows the same line of development as *Gastrodia* (Kusano, 1915). In this plant it has been shown that the micropylar cell from the first division fails to divide thus forming a row of three cells. The innermost of these becomes the functional megaspore, while the outer two cells degenerate. The nucleus of the megaspore divides twice to form a four nucleate embryo-sac like that found in *C. Pringlei.* The four nuclei form two synergids, an egg, and one polar nucleus. This same mode of development of the embryo-sac is found in *Oenothera, Godetia* and *Epilobium* (Ishikawa, 1918). In *Commelina stricta* the embryo-sac consists of eight nuclei. Two potential megaspores divide to form the embryo-sac.

Kusano (1915) reports that in *Gastrodia*, the one polar nucleus fuses with one synergid and the second male nucleus to form the triploid endosperm nucleus. In *Oenothera*, Ishikawa (1918) reports that the endosperm nucleus arises from the fusion of the male nucleus with the single polar nucleus thus giving a diploid condition. Definite information on the origin of the endosperm in *C. Pringlei* was not obtained, but it is of the free nuclear type.

Bergdolt (1932) has made careful quantitative studies in certain species of *Viola* to determine the effect of various external factors upon cleistogamy and chasmogamy. In general he finds a marked response to soil conditions, showing a conspicuous decrease in cleistogamy with increased

fertility. It was also shown that, contrary to the findings of Vöchting and others, poor light conditions showed a reduction in the numbers not only of chasmogamous flowers but also of cleistogamous flowers. Also under ordinary soil conditions seedlings of *Viola* species show only cleistogamous flowers during most of their first year's growth.

From his results it is seen that with *Viola*, the nutritional factor is the most influential in determining the proportion of cleistogamy and chasmogamy. It is very difficult to compare other data on cleistogamy with Bergdolt's for most observations on the prevalence of cleistogamy are not based upon quantitative counts and little attention has been paid to soil condition, age of the plants, and other factors connected with flowering. From the literature on the subject it would seem however that the results on *Viola* do not necessarily apply to other plants. Those cleistogamous species in which chasmogamy has not been observed, according to Knuth (1906), are apparently influenced by external conditions so far as the proportion of cleistogamy is concerned.

The early growth of a crescent shaped constriction in the outer integument of *Commelianantia* results in the separation of the sporangium into a relatively small micropylar region and a very large chalazal region. This separation persists so that at the maturity of the seed the embryo occupies the micropylar region and the endosperm, the chalazal region.

This type of seed seems to be characteristic of the Commelinaceae. The seeds of both *Commelina* and *Tradescantia* are essentially the same as those of *Commelinantia*. The embryo is in a sense isolated from the endosperm since at the maturity of the seed there is no recognizable endosperm surrounding it. The embryo and endosperm of these seeds would seem to have little influence upon one another at any time during their development.

Vöchting (1893) experimented with the effect of a deficiency of light on chasmogamous flowers. As a result of these experiments he found that with some plants as, for example, *Stellaria media* and *Lamium purpureum*, which under ordinary light conditions are chasmogamous, conspicuous parts are imperfectly developed and the flowers remain closed in feeble light. In these plants, Vöchting believed, chasmogamous and cleistogamous flowers may be produced at will.

The comparative study made by Miss Ritzerow (1908) over a wide range of families led her to believe that cleistogamous forms are chasmogamous forms which have been retarded in their development. These flowers follow the course of development of the normal flowers. She finds that in many cases there is a reduction in the number of fertile stamens, a

reduction in the number of pollen sacs per stamen, and the corolla may be either greatly reduced or lacking. In her extensive study of pollen germination she finds that the anthers may dehisce and allow pollen to escape or the pollen may remain in the anthers after dehiscence, or the anthers may not dehisce. If the anthers do not dehisce, the tubes grow through the anther walls and make their way to the stigma.

The large number of transitional stages in the Austin material of *C. Pringlei* as contrasted with the apparent excess of aerial cleistogamous flowers from the Mexican material as has been mentioned may have been due to some differences in growth conditions. Although both sets of material were collected in the winter it is quite possible that the plants were grown under quite different conditions of soil, light, and temperature.

SUMMARY

1. *Commelinantia Pringlei* produces chasmogamous flowers on the upper portion of the plant, smaller, transitional flowers at the base of the plant, and cleistogamous flowers below the surface of the ground.

2. Cleistogamous flowers of *C. Pringlei* will open if exposed to light, but the petals are reduced in size and the stamens and pistil have the characteristics of those cleistogamous flowers which have not been induced to open.

3. Early in the development of this flower the ovary is spherical and the ovules lie back to back in the same horizontal plane. The ovary elongates as it matures and the ovules come to lie above one another.

4. Their anthers dehisce, but very little pollen is found outside the anther cavities. The pollen grains germinate wherever they lie and the pollen tubes make their way to the stigmas.

5. In *C. Pringlei* three cells have been formed after the second reduction division is complete. The micropylar cell of the first division fails to divide and the two inner cells arise from the division of the inner cell of the first division.

6. The inner cell of the three becomes the functional megaspore, which undergoes two divisions to form a four-celled embryo-sac.

7. A crescent shaped constriction in the outer integument is formed early in the development of the sporangium and persists throughout its development.

8. An enormous enlargement takes place in the chalazal end of the sporangium, while but slight growth occurs on the micropylar side of the constriction.

9. At maturity, the endosperm occupies the chalazal portion of the sporangium and the embryo occupies the micropylar portion.

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Explanation of plates

The drawings were made by the aid of a camera lucida. The following letters are used to designate the parts of the flower in plate 7: S, sepals; P, petal; ST, stamen; C, carpel; O, ovule; STY, style; STI, stigma; A, anther; SH, sheathing bract; B, protective bract.

Plate 7

Fig. 1. A very young flower showing the primordia of sepals. ×24.

Fig. 2. A young flower bud showing the two sheathing bracts and the protective bract. The sepals appear as lobes on the central mass. ×24.

Fig. 3. Protective bract covering the growing sepals. ×24.

Fig. 4. This section shows the greatly enlarged sepals and the primordia of the stamens. ×24.

Fig. 5. The sepals enclose the bud. The stamens are enlarged at the upper ends. The petals appear. ×24.

Fig. 6. This section shows two of the three carpels which are formed. ×24.

Fig. 7. The sepals are quite large. The petals surround the other structures. The anthers are beginning to differentiate. ×24.

Fig. 8. The sepals, petals, and anthers are enlarged. The carpels are distinct. ×24.

Fig. 9. The sporogenous tissue of the anthers is distinct. The ovules appear. The carpels have fused incompletely to form the hollow style. ×24.

Fig. 10. The anthers are enlarged. The beginning of a style appears . ×24.

Fig. 11. The pollen is mature in the anthers. The style is slightly elongated. ×24.

Fig. 12. This section of an older flower bud shows the presence of a glandular stigma. The ovules show the megaspore mother cell in synapsis. ×24.

Fig. 13. The elongated ovary showing two ovules, one above the other in one of the cavities. ×14.

Fig. 14. Section of an older pistil showing the hollow bent style and glandular stigma. ×24.

Fig. 15. This section shows a flower just before fertilization. The sepals and petals are withering away. The anthers are dehisced, the style is bent, and the ovary is pushing out of the withering floral parts. ×8.

Fig. 16. A cross section showing the glandular stigma and the dehisced anthers. Pollen grains just beginning to germinate and some whose tubes have reached the stigma are seen near the anthers. ×125.

Fig. 17. A mature capsule. Notice the withered style and stigma. This capsule contains two seeds on one side while the other side is empty. ×8.

Plate 8

Fig. 1. Megaspore mother cell in synapsis. Parietal cells are seen between the mother cell and the epidermis. ×345.

Fig. 2. Megaspore mother cell recovering from synapsis. ×345.

Fig. 3. Metaphase of the first reduction division. ×345.

Fig. 4. Two cells resulting from the first reduction division. ×345.

Fig. 5. Metaphase of the second reduction division. The outer cell from the first division remains undivided. ×345.

Fig. 6. Two megaspores and one cell from the first division. The upper two cells are beginning to degenerate. ×345.

Fig. 7. Functional megaspore with the remains of the two degenerating cells. ×345.

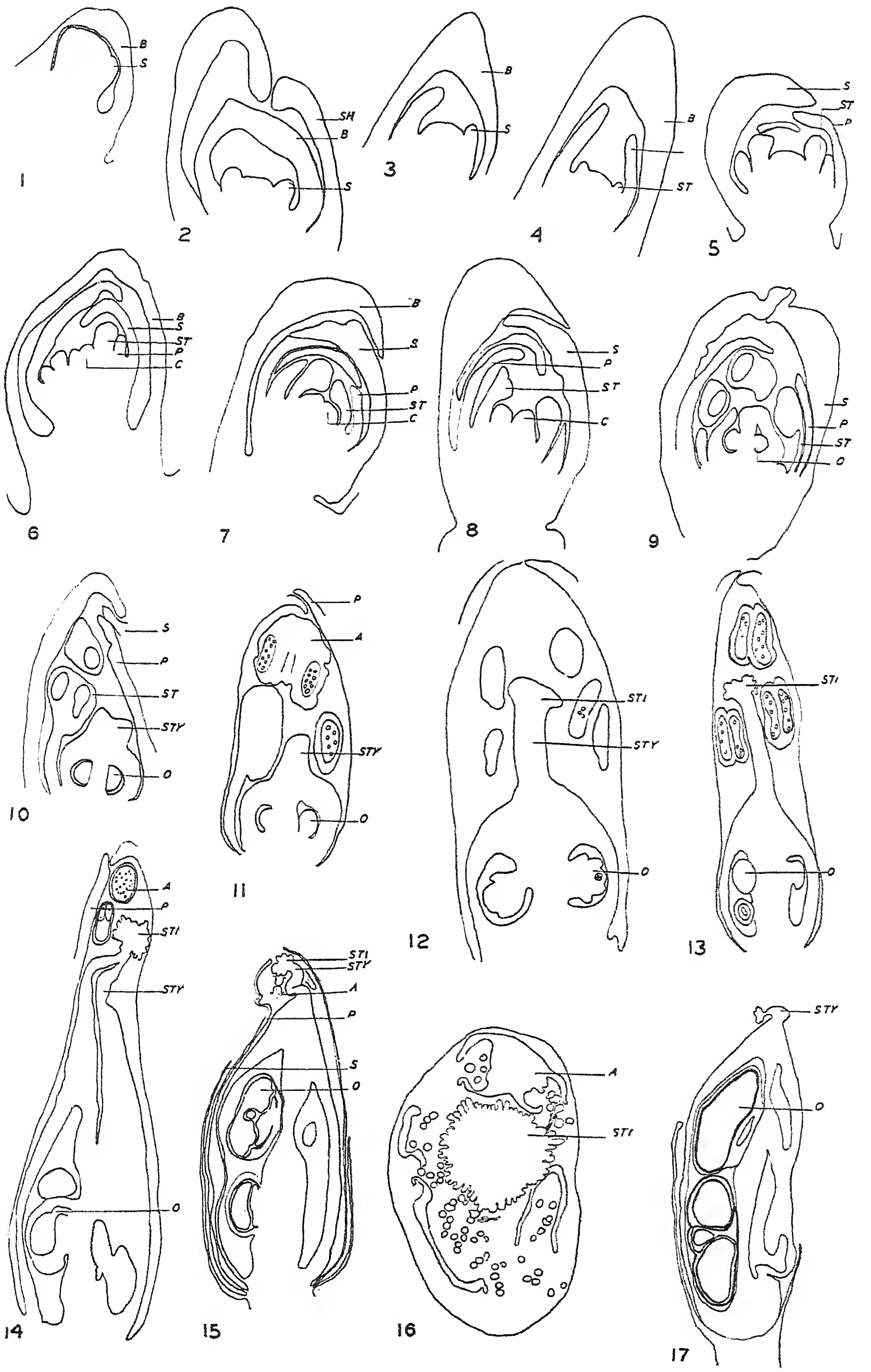
Fig. 8. First division of the megaspore. A remnant of the upper cell still remains. ×345.

Fig. 9. The two embryo-sac nuclei move to opposite ends of the sac. The remainder of the upper cells becomes a faint line. ×345.

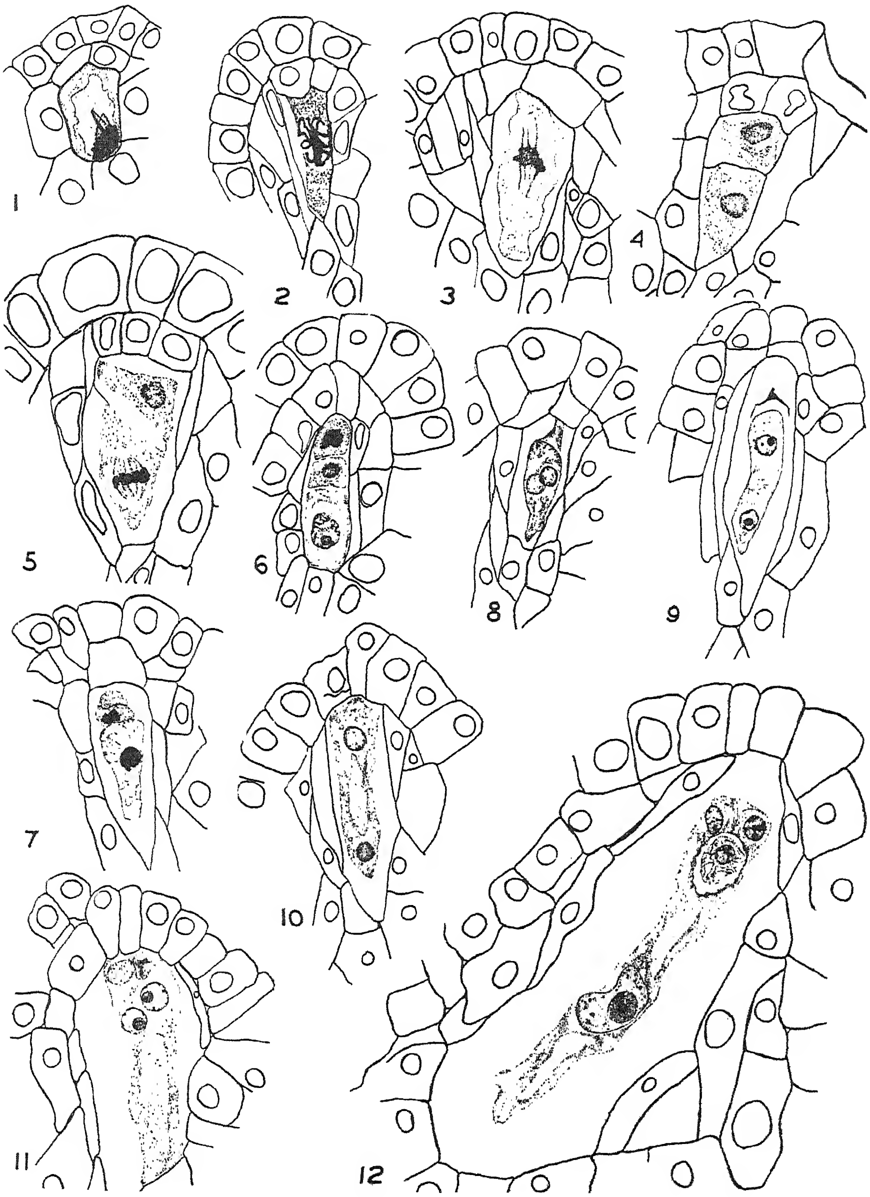
Fig. 10. Two-nucleated embryo-sac. The nucellus has begun to be digested. ×345.

Fig. 11. The embryo-sac nuclei have migrated to the upper end of the sac. ×345.

Fig. 12. Nearly mature embryo-sac. No membranes are found around egg and synergid. ×345.



PARKS: COMMELINANTIA



PARKS: COMMELINANTIA

INDEX TO AMERICAN BOTANICAL LITERATURE
1931–1934

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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To the Memory of This
DISTINGUISHED LEADER IN BOTANICAL SCIENCE
This Volume is
Affectionately Dedicated

The dedicatory page is contributed by John Hendley Barnhart, Bibliographer of the New York Botanical Garden and friend of long standing.

The portrait of Doctor Britton is reproduced from a photograph taken 22 June 1902 in the herbarium of the New York Botanical Garden by the staff photographer, Mr. F. Berte.

A recessive factor lethal for ascospore formation in Neurospora

B. O. Dodge

(WITH PLATES 9 AND 10)

Ascus abortion in an x-rayed line of *Neurospora tetrasperma* was recently reported (Dodge, 1934) as due to a "lethal" which prevents the delimitation of ascospores and which segregates at meiosis. The lethal can not be maintained continuously in a haploid mycelium unless the nucleus which carries it is accompanied by a normal nucleus. Ascus abortion in the case described, therefore, occurs in an ascus heterozygous for the lethal. The present paper deals with a very different type of ascus abortion, an abortion which is due to a recessive gene, lethal in an ascus homozygous for this factor so that no ascospores are formed and the ascus sac itself finally disintegrates.

HOMOZYGOUS ASCUS ABORTION

Among the 1-ascospore cultures obtained by mating the mycelium from the x-rayed ascospore, G5.3, with normal race S1, was one (G5.3×S1) 9, that showed signs of reversion to normal. Testing out a number of 1-ascospore races from this mating, it was found that one race (G5.3×S1) 9.7, referred to hereafter simply as 9.7, developed perithecia very slowly at first, but later, it, as well as sub-cultures from it, matured perithecia much more rapidly. Although a great many fruit bodies, fairly normal in appearance, always develop in such cultures, and many asci reach full size in every case, the asci all abort, so that very few, if any, ascospores are ever formed (plate 9,C). The large hyaline highly refringent bodies in these aborting asci might be mistaken for spores. Lindegren (1934) unfortunately refers to some such bodies in an ascus of *N. crassa* as spores without nuclei. As will be shown cytologically, in our material they are merely vacuoles. In old cultures the perithecial cavity is filled with a rather formless mass of disintegration products. Sometimes the contents burst through the perithecial wall or through the ostiolar region to show as a whitish drop on the outside. Occasionally one finds a heavily indurated dark colored empty ascus, and more rarely a body that may represent an abnormal ascospore.

Since asci in perithecia of race 9.7 do not delimit spores, how can the race be bred? One can transfer to sub-cultures in the old way, but such transfers will be just like the original 9.7; they will, in fact, still be the original. There are, however, two different ways by which this race can be bred sexually so that its nature can be studied effectively. First, it can be

[THE BULLETIN FOR FEBRUARY (62: 65–115) WAS ISSUED FEBRUARY 1, 1935]

grown in plate cultures opposite a normal unisexual race. The writer (Dodge, 1931) has shown that hermaphroditic races of *Neurospora* can be crossed or hybridized with unisexual races in this way. This method was recently tried out with some of the hermaphroditic races such as (G5.3×S1) 4.38 originating from the x-rayed series and which carry the first type of lethal for spore formation and ascus abortion (see plate 9,A). If the normal unisexual race opposed is of the sex opposite that of the normal nuclei in the hermaphroditic race, then two kinds of perithecia will be found. In addition to those containing indurated aborted asci produced on the hermaphroditic mycelium, there will be some normal perithecia without any sporeless indurated asci whatever. But if the unisexual race opposed is of the sex opposite to that of the lethal nuclei carried along in the hermaphroditic mycelium, then the perithecia are all alike and will all contain some aborted asci. On certain potato dextrose agars in tube cultures most of the asci abort, but on corn meal agar the lethal action is not complete so that ascospores sufficient for breeding purposes are produced, and it is not necessary to resort to this method of plate culturing.

In case of race 9.7 where, even under the most favorable conditions yet found, very few, if any, true ascospores are formed, the plate method proved valuable. When 9.7 was grown in a plate opposite normal unisexual races such as S1, sex B, and S6, sex A, perithecia with asci bearing spores were formed regardless of the sex of the normal race opposed. This proved that the 9.7 mycelium contains nuclei of opposite sex and suggested that these nuclei also carry something that prevents spore formation when two of them are united in an ascus; a nucleus of either kind, however, united with a normal nucleus of the opposite sex in an ascus becomes inoperative to produce abortion. Spores are then delimited. Since the mycelium is heterokaryotic sexually at least, perhaps something could be learned after all by studying its conidia to see how many kinds are formed and how mycelia derived from them would react in cultures of various sorts.

Conidial isolates from mycelium 9.7

Conidia from culture 9.7 were sowed in the usual way (Dodge, 1928b) and thirty-two 1-conidium isolates were obtained. In making the selections, the smaller and more slowly growing conidia were chosen in order to obtain unisexual mycelia. Twenty-three of the isolates proved to be hermaphroditic, each developing many perithecia, but in each case all of the asci aborted just as would be expected. The cultures were observed for the next four months without finding any changes except further degeneration.

The other nine isolates were unisexual. They were grown together in all possible combinations, and it was found that nos. 9.7C1, 9.7C4 and 9.7C5 were alike and of the same sex reaction, while 9.7C2, 9.7C3, 9.7C6, 9.7C7, 9.7C8 and 9.7C9 were of the opposite sex. The resulting perithecia contained great numbers of asci but no spores. Ascus abortion was complete. Each isolate was then in turn grown with the S1 tester, sex B, and the new S9 tester, sex A. Those of the first group proved to be sex A, and those of the second group sex B. The perithecia formed in these test cultures all bore asci with spores (plate 10,B).

It may be recalled that normal bisexual races of *N. tetrasperma* (Dodge, 1928b) produce three kinds of monilioid conidia. It has also been proved more recently that any bisexual race from the irradiated line G5.3, which produces the type of aborting asci shown in plate 9,A, also develops three kinds of monilioid conidia, but only two of the kinds are able to function vegetatively. Some are bisexual and their mycelia produce perithecia with the indurated aborted asci. Other conidia are unisexual and normal, that is, their nuclei do not carry the lethal; in any particular culture they are all of the same sex. Conidia carrying only lethal or deficient (?) nuclei are also abstricted, but they die soon after they germinate. In this respect they are just like the unisexual ascospores that carry only lethal nuclei.

Proof of a mutation or genetic change

Many cases of variations or saltations found in the mycelial and fruiting characters of the fungi have been referred to as mutations without any real evidence. Dixon (1933) shows some interesting effects of irradiating ascospores and mycelia of *Chaetomium*. His saltant mycelia in some cases produced numerous perithecia which matured spores, but the author did not prove the saltation to be genetic and hereditary. By testing out the ascospore progeny one could have seen whether the changes brought about by the irradiation were nuclear and hereditary and not merely cytoplasmic. For example, ascus abortion in case of our 9.7 race is not proved to be genetic even when mycelia obtained from its conidia are mated. On the contrary, it would at first seem to be merely cytoplasmic because ascospores in abundance mature when the conidial isolates are mated with normal tester races. Only when these f_1 ascospores are analyzed is it shown that the factors for this new type of ascus abortion are also segregated at meiosis and are hereditary.

Starting with culture 9.7C8$\times$S9, fifty-six f_1 1-ascospore cultures were isolated. The small, and therefore unisexual, spores were selected where possible. Cultures nos. −1, −4, −9, −14, −53, −54, and −56, proved to be hermaphroditic and their perithecia mature asci with spores. The common

parental mating formula (9.7C8×S9) may be omitted. Nos. −3, −13, −19, −25, −27, −32, −33, −34, −42, −46, and −52 either died after germinating, or produced merely dwarf mycelia. These were eventually discarded without further test although they would have been interesting genetically. Nos. −7, −15, and −24 were lost accidentally. The other thirty-five races were mated against testers S1 and S9. Twenty-four proved to be of sex A and eleven sex B in their reaction. In all cases the resulting perithecia here also produced asci with spores. There were several cases of rather weak sexuality shown and some spore abortion but no case of complete lack of spores from ascus abortion such as characterizes race 9.7.

Back-crossing f_1 progeny with unisexual components of race 9.7

It usually requires from three to five days to get positive reactions. Ascospores begin to form about the sixth or seventh day. Some combinations fruit much more slowly. Each of the eleven sex B f_1 clones was mated against each of the three sex A conidial isolates from 9.7. The following sample matings, taken from the record, but omitting the details, illustrate the method of procedure. Only matings of clones of opposite sex are given here. The sign + means that perithecia were formed.

9.7C1×(9.7C8×S9) 5 = +, very strong reaction, many ascospores.
9.7C4×(9.7C8×S9) 5 = +, very strong reaction, many ascospores.
9.7C5×(9.7C8×S9) 5 = +, very strong reaction, many ascospores.
9.7C1×(9.7C8×S9) 8 = +, rather incompatible, complete ascus abortion.
9.7C4×(9.7C8×S9) 8 = +, very incompatible, complete ascus abortion.
9.7C5×(9.7C8×S9) 8 = −, completely incompatible in this culture.
9.7C5×(9.7C8×S9) 8 = +, weak sexuality, but complete ascus abortion.
9.7C1×(9.7C8×S9)12 = +, very strong, many ascospores.
9.7C4×(9.7C8×S9)12 = +, very strong reaction, many ascospores.
9.7C5×(9.7C8×S9)12 = +, very strong, many ascospores.
9.7C1×(9.7C8×S9)26 = +, very strong reaction, but complete ascus abortion.
9.7C4×(9.7C8×S9)26 = +, very strong, but complete ascus abortion.
9.7C5×(9.7C8×S9)26 = +, very strong, complete ascus abortion.
9.7C1×(9.7C8×S9)43 = +, very strong reaction, many ascospores.
9.7C4×(9.7C8×S9)43 = +, strong, many spores.
9.7C5×(9.7C8×S9)43 = +, very strong reaction, many spores.

These sample matings show that certain combinations resulted in the development of perithecia with asci but the asci aborted without delimiting spores. Other combinations gave what appeared to be perfectly normal perithecia with an abundance of spores. It is also evident that the three

conidial isolates 9.7C1, 9.7C4 and 9.7C5 are alike; they are the same clone in fact.

Each of the twenty-four f_1 sex A races was mated against the conidial isolate 9.7C2 which is sex B. The results were of the same nature. Some combinations gave normal perithecia with many ascospores, others produced fruit bodies with many asci but these all aborted without forming spores. Cases of weak sexual reactions were represented as before.

Judging from the results of the reactions there were four very definite classes of the f_1 ascospore progeny from the mating (9.7C8×S9). This was proved out further by mating or inbreeding the twelve sex B f_1 ascospore races in various combinations with the twenty-three sex A f_1 ascospore races so that each race was used at least once in some combination. A race derived from an ascospore is a definite clone and it is called here an ascospore race to distinguish it from a conidial isolate of 9.7. Four sample matings are given below.

(9.7C8×S9) 2×(9.7C8×S9) 8=+, complete ascus abortion.
(9.7C8×S9) 6×(9.7C8×S9)10=+, strong reaction, complete ascus abortion.
(9.7C8×S9) 6×(9.7C8×S9)22=+, rather weak, but ascospores.
(9.7C8×S9) 6×(9.7C8×S9)44=+, strong, many ascospores.

The results of a number of such matings in which every one of the thirty-five f_1 haplont clones was tested, proved conclusively that the factors responsible for ascus abortion are recessive, are segregated at meiosis and are therefore hereditary.

In order to further prove that the lethal carried by the conidial isolate clone 9.7C4, which is sex A, is the same as that carried by the isolate 9.7C8, sex B, a number of the f_1 progeny of the mating 9.7C4×S1 were also analyzed. A few of the results are given below. It should be held in mind that the thirty-five f_1 ascospores previously analyzed were from the mating 9.7C8×S9.

f_1 ascospore progeny of 9.7C4×S1 mating

From the mating 9.7C4×S1, fifty 1-ascospore f_1 clones were obtained in the usual way. Three germinating spores died after having been transferred. Eighteen mycelia turned out to be bisexual. The resulting perithecia all bore asci with spores. Twenty-nine of these f_1 clones were unisexual, thirteen being sex A and sixteen sex B.

Forty-one matings were then made, crossing the progeny of the mating 9.7C4×S1 with progeny of the mating 9.7C8S9. A few sample matings are given here to again indicate the method.

(9.7C8×S9)26×(9.7C4×S1) 4=+, asci with spores.

(9.7C8×S9)18×(9.7C4×S1) 1=+, asci with spores.
(9.7C8×S9)26×(9.7C4×S1)16=+, with aborted asci only.
(9.7C8×S9) 6×(9.7C4×S1)39=+, with aborted asci only.
(9.7C8×S9)36×(9.7C4×S1)36=+, asci with ascospores.

Furthermore the f_1 progeny of the mating 9.7C4×S1 were inbred in twenty-five different combinations in the way the sample matings below indicate.

(9.7C4×S1) 8×(9.7C4×S1) 2=+, with aborted asci only.
(9.7C4×S1)14×(9.7C4×S1) 2=+, with aborted asci only.
(9.7C4×S1)16×(9.7C4×S1)46=+, asci with spores.
(9.7C4×S1)16×(9.7C4×S1)43=+, perithecia with aborted asci.

The results of all of these matings show that the f_1 progeny of the mating 9.7C4×S1 fall into four classes as do the progeny of the mating 9.7C8×S9. Whenever there is a mating between two clones each of which carries the same factor for ascus abortion, the ascus is homozygous for this factor, no spores are formed and ascus abortion is complete (plate 9, C). If one of the parents is normal, that is, non-lethal, and the other carries the factor for abortion, then the asci in the resulting perithecia are heterozygous for this factor and cut out spores as shown in plate 10, B.

For convenience merely, we have in the past designated the particular sex reactions of heterothallic clones of *Neurospora* by the letters A and B instead of by the signs + and −. As has been pointed out a number of times by the writer, normal or wild type races usually produce not only incipient perithecia in culture but also spermatia (microspores or microconidia). Both types of conidia function asexually in propagation, and both types function sexually as fertilizing elements. The fact that the spermatia will germinate to form perfectly normal mycelia and that the monilioid conidia serve beautifully as "spermatizers" (Dodge, 1932) has puzzled certain recent writers on this subject, and as such unorthodox behaviors do not fit into their categories they have ignored them altogether.

In the language of the geneticist it would certainly be much simpler to refer to the factors for sex reactions not as A and B, but as S and s, or some other pair of letters. Since we have always referred to our sex A and sex B tester strains as S9 and S1 respectively we shall in this instance use "A" and "a" to avoid confusion, "A" for the sex A factor and "a" for the sex B factor.[1] They are clearly fundamental factors governing the sex reactions and they are allelomorphic. We may also refer to the normal factor combination or condition whatever it may be, for delimitation of asco-

[1] See also Hans Zickler in Planta 22: 573–613, 1934, for a paper which has just come to hand too late for consideration here.

spores as L and the comparable inhibiting combination or gene as l, so that the four classes of clones discussed above may be designated by the symbols AL, aL, Al, and al. AL×aL gives normal ascospore production. Al×al results in complete ascus abortion. AL×al and Al×aL give ascospores. In a large population there should then be a three to one result: three combinations maturing asci with spores to one in which the asci abort completely without forming spores. The following shows the number in each class, grouping the progeny of the mating 9.7C4×S1 together and those of mating 9.7C8×S9 in a second group. The parental formula which should precede the number designating the particular f_1 clone is omitted in each case for the sake of brevity.

f_1 progeny of mating (9.7C4×S1)

AL: 1, 4, 25, 27, 30, 31, 35, 41, 44 (nine in all)
aL: 10, 12, 23, 36, 38, 40, 42, 45, 46, 50 (ten in all)
Al: 8, 14, 16, 48 (four in all)
al: 2, 3, 26, 34, 39, 43, (six in all)

f_1 progeny of mating (9.7C8×S9)

AL: 29, 30, 31, 37, 40, 41, 48, 49, 51, 55 (ten in all)
aL: 5, 12, 22, 23, 43, 44 (six in all)
Al: 2, 6, 16, 17, 20, 28, 35, 36, 38, 39, 45, 47, 50 (thirteen in all)
al: 8, 10, 11, 18, 21, 26 (six in all).

Summarizing, the mating tests show that: (1) any clone AL in either group, mated with any clone aL in either group, will give normal perithecia with asci containing normal spores; (2) any combination AL×al or any Al×aL mating will give perithecia with asci containing spores; and (3) any Al×al mating will give perithecia with all asci aborted. Due allowance should be made where, in a few cases, weak sex reactions come into play to slow down perithecium production. With sufficiently large populations the ratio of these matings that result in perithecia with ascospores to those resulting in complete ascus abortion should then be about 3:1.

One has only to recall the simplest case of albinism in maize to understand the genetics of this type of ascus abortion. Maize seedlings heterozygous for a recessive lethal for chlorophyll are green, but seedlings homozygous for the factor are white and soon die. Self-pollinated heterozygous plants give offspring in a 3:1 ratio, three green to one white.

LINKAGE

When grown on dextrose agar media the f_1 progeny classified above show some very striking differences in their cultural characteristics which

are not so apparent when they are grown on a corn meal agar. Some cultures develop a whitish more or less appressed aerial growth and the medium turns blackish at the surface. Other cultures develop an abundance of orange-colored conidia while the agar medium maintains its clear amber color for some time. The ratio of the number of the former to the number of the latter kind was 3:1. When the sex reaction and the presence or absence of the lethal factor, l, were considered it was seen that all of the clones showing the bright orange masses of conidia belong to the same particular group aL of the four classes as arranged above. The progeny of both matings, (9.7C4×S1) and (9.7C8×S9) showed the same differences.

As suggested to the writer personally by Dr. A. F. Blakeslee and again by Prof. E. W. Sinnott, this looks as though some factor or combination, say O, for orange-colored masses of conidia is inhibited by the same recessive lethal, l, which when homozygous also prevents ascospores formation. This factor O is linked with the sex reaction factor a, so that, introducing the symbols O and o, the four classes of clones would be indicated as follows: (Ao)L, (aO)L, (Ao)l, and (aO)l. The second class, (aO)L is the only kind that could produce the bright orange-colored masses of conidia because in the combination (aO)l the factor O is suppressed in its activities by the lethal factor l.

This would be in line with what has been pointed out before (Dodge, 1928a; 1928b) to the effect that the tester race S1 ("a") always seems to produce more of the orange-colored conidia than does race S6 ("A"). Our new tester S9 ("A") which was used in the present work is similar in this respect to S6. No proof that this character for conidia is linked has ever been offered however. In *Neurospora sitophila* albino non-conidial races such as 56.1 and 56.2 reacting as "a" were readily obtained (Dodge, 1930; 1931). Certain interspecific hybrids that would pass for *N. tetrasperma* were bred up so that one of the two unisexual components of a bisexual race was non-conidial and "a" in its sex reaction at the same time. Lindegren (1932) has suggested that there may be some linkage relations involving color character, the production of conidia, conditions for ascospore germination and sex reactions in the hybrids just referred to. Furthermore Lindegren (1933) has proved a linkage between the sex factor and "*pale*" in *Neurospora crassa*. Mr. F. L. Tai, who is working on this question in our laboratory, will publish his results in due time.

NUCLEAR BEHAVIOR IN ABORTING ASCI

Normally nuclei of *Neurospora tetrasperma* pair up after the third division in the ascus and cut out the spores, one nucleus of each sex going

to each spore. A fourth division occurs as the spores mature (Dodge, 1927). In case of those abnormal asci (plate 9, A) where abortion occurs in an ascus heterozygous for a lethal or deficiency, nuclear fusion occurs as usual, but the cytoplasm of the full grown ascus is apt to be very foamy and vacuolate (plate 10, G) and this disintegration may set in before the third division. The reduction divisions are certainly very abnormal and clear cut cases of the first, second, and third divisions are hard to make out. They are not always simultaneous and show many other irregularities. Several preparations show that the eight nuclei resulting from the third division may all divide again without cutting out any spores. Such asci invariably abort. The sixteen nuclei degenerate (plate 10, F, G), and the ascus sac begins to thicken and becomes dark colored. Occasionally the reduction divisions are sufficiently normal to allow for the delimitation of ascospores and we are thereby provided with a sufficient number for breeding purposes.

In case of those asci shown in plate 9, C and plate 10, A, where the abortion is due to a recessive factor that is effective to prevent ascospore formation only when in an ascus homozygous for this factor, preparations show that nuclear fusion and the three divisions occur rather normally. The eight resulting nuclei then move to the center of the ascus as though crowded into that position by the pressure of the enlarging vacuoles on either side (plate 10, C–E). The nuclei then all slowly degenerate. The nature of the hyaline bodies that look so much like spores in the asci (plate 9, C) is clear from the cytological preparations. They are merely vacuoles. Occasionally the eight degenerating nuclei are separated into two or three groups by intervening vacuoles (plate 10, C).

There is some evidence that the nuclei in these aborting asci may rarely undergo a fourth division before they degenerate. This may account for the few cases where one finds an aborted thickly indurated ascus among the colorless asci in the perithecia of race 9.7. Any temporary condition of the culture that would lead to a fourth precocious nuclear division may be all that is necessary to bring about the type of abortion where the ascus sac becomes indurated. This would not necessarily be a genetic change such as would be inherited like those illustrated in plate 9, A. Anything that would speed up the nuclear divisions so that a fourth division would occur before the spores could be cut out might prevent the normal working of the machinery concerned with spore delimitation. Or, to put it another way, there seems to be something in all of the species of *Neurospora* so far found that inhibits this fourth division until *after* the spores are formed, then it is allowed to take place. Suppress or remove the inhibitor and the differentiations that give the ascospores their wall characteristics are

applied, in the absence of ascospores, to the ascus sac itself which then becomes darkly colored, thick walled and striated much like mature giant ascospores. It would not be surprising to find that under certain conditions such asci if taken early enough would actually germinate! Sections show that they are quite devoid of nuclei and cytoplasmic contents after they have become fully indurated.

We have several species of ascomycetes, notably among the Ascobolaceae where the asci have more than eight spores, which means that there are regularly more than three nuclear divisions before spore formation. Some species have asci with sixteen spores, others have asci with thirty-two spores and so on up to *Thelebolus* where there must be ten successive nuclear division before the 1024 spores are cut out. This behavior is the normal procedure, however, for those species and particularly characterizes each one.

Ascus abortion of the type which ends with induration, then, can be genetic and heritable, or it can be a temporary and abnormal development not transmitted to the next generation, as reported previously (Dodge, 1934). The first type was evidently due to the effects of irradiating the parental ascospore. In the other cases mentioned at that time the abortion must have been due to some abnormal cultural condition which affected the fungus only locally and temporarily. Ascus abortion of the type described in the present paper is genetic and complete but it should be distinguished from cases of parthenocarpy where perithecial bodies without any asci are formed in cultures of race G5.3 when grown alone.

SUMMARY

Among the progeny derived from a mating of two mycelia, one of which had come from an x-rayed ascospore of *Neurospora tetrasperma*, was a bisexual clone 9.7 which develops perithecial fruit bodies containing numbers of asci, but these asci abort without forming ascospores. The mycelium of clone 9.7 develops three kinds of monilioid conidia. Some are bisexual and their mycelia will mature perithecia likewise with only aborting asci but no ascospores. The other conidia are unisexual. Mating their mycelia together in different combinations it was found that they were of two kinds sexually. Here the fertile matings gave perithecia with only aborted asci the same as clone 9.7 itself. Mating these unisexual clones with tester races S1 and S9 it was found that the fertile combinations always gave perithecia whose asci delimited ascospores. Analysis of these 1-ascospore clones proved that they were primarily of four sorts genetically, AL, aL, Al, and al, where A and a represent sex reaction or sterility factors and L and l represent factors governing the delimitation

of ascospores, l being recessive and lethal for spore formation in an ascus homozygous for it. The ratio of the number of matings that give perithecia with ascospores to the number of matings that give perithecia with only aborting asci theoretically should be about 3:1. In such an aborting ascus homozygous for l, nuclear fusion is followed by three successive nuclear divisions after which the eight nuclei move to the center of the ascus and slowly degenerate.

The f_1 ascospore clones when grown on certain dextrose media showed striking cultural differences in a ratio about 3:1. Three-fourths of the cultures or clones produced a rather limited amount of whitish, sometimes appressed, aerial growth with few conidia, and the medium was blackened. One-fourth of the clones produced bright masses of orange-colored conidia, and the medium maintained its clear amber color for some time. Such clones all fall in the group aL suggesting that there may be a factor which we may call "O" concerned with the type of growth, abundance of conidia and certain color effects, and which is linked with the sex reaction factor "a". This factor O is inhibited by the recessive factor "l" which is also lethal for ascospore formation when homozygous. In any series of the f_1 progeny one fourth, (aO)L, of the cultures will produce an abundance of bright orange-colored conidia while the other three fourths (Ao)L, (Ao)l, and (aO)l produce few conidia and a whitish more or less appressed aerial growth and the medium often becomes blackened.

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Explanation of plates 9 and 10

Neurospora tetrasperma

Plate 9

A. Reproduced from the writer's previous paper (1934) for comparison. Aborted asci are heterozygous for a lethal or deficiency resulting from irradiating a parental ascospore. Each of the spores in the 4-spored asci is provided at its origin with one nucleus carrying the lethal and one normal nucleus of opposite sex. In the 8-spored ascus, four spores are normal and four would carry only lethal nuclei and would die soon after germination.

B. Normal asci such as would develop when two mycelia derived from two of the normal spores of opposite sex shown in the 8-spored ascus in A are mated. The insert, lower right, shows a 5-spored ascus. The two small spores would be unisexual.

C. Aborted asci homozygous for a recessive factor, l, lethal for spore formation only when homozygous. The large hyaline spore-like bodies are merely vacuoles. Asci heterozygous for this factor delimit ascospores as shown in plate 10, B.

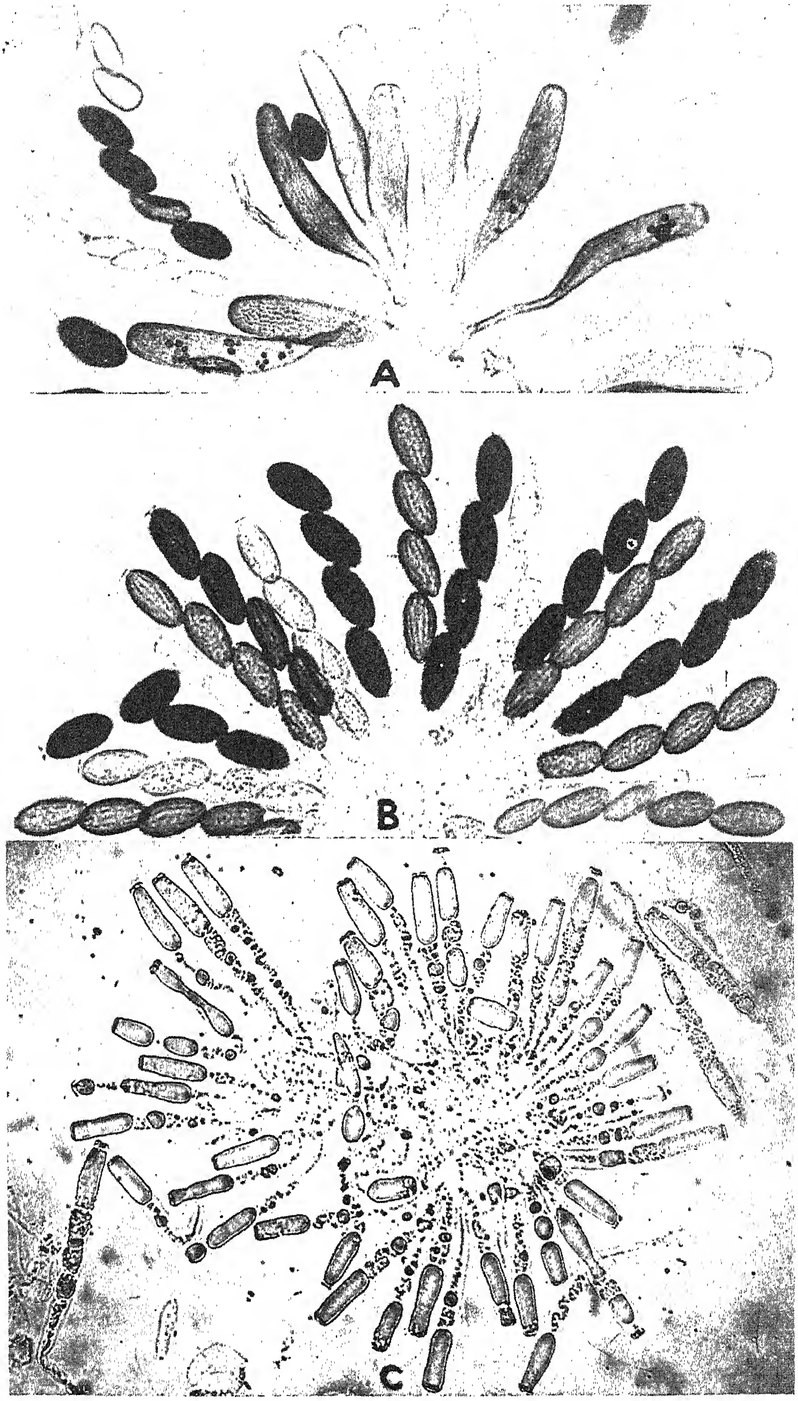
Plate 10

A. Young aborting asci homozygous for the recessive factor l. Compare with B below.

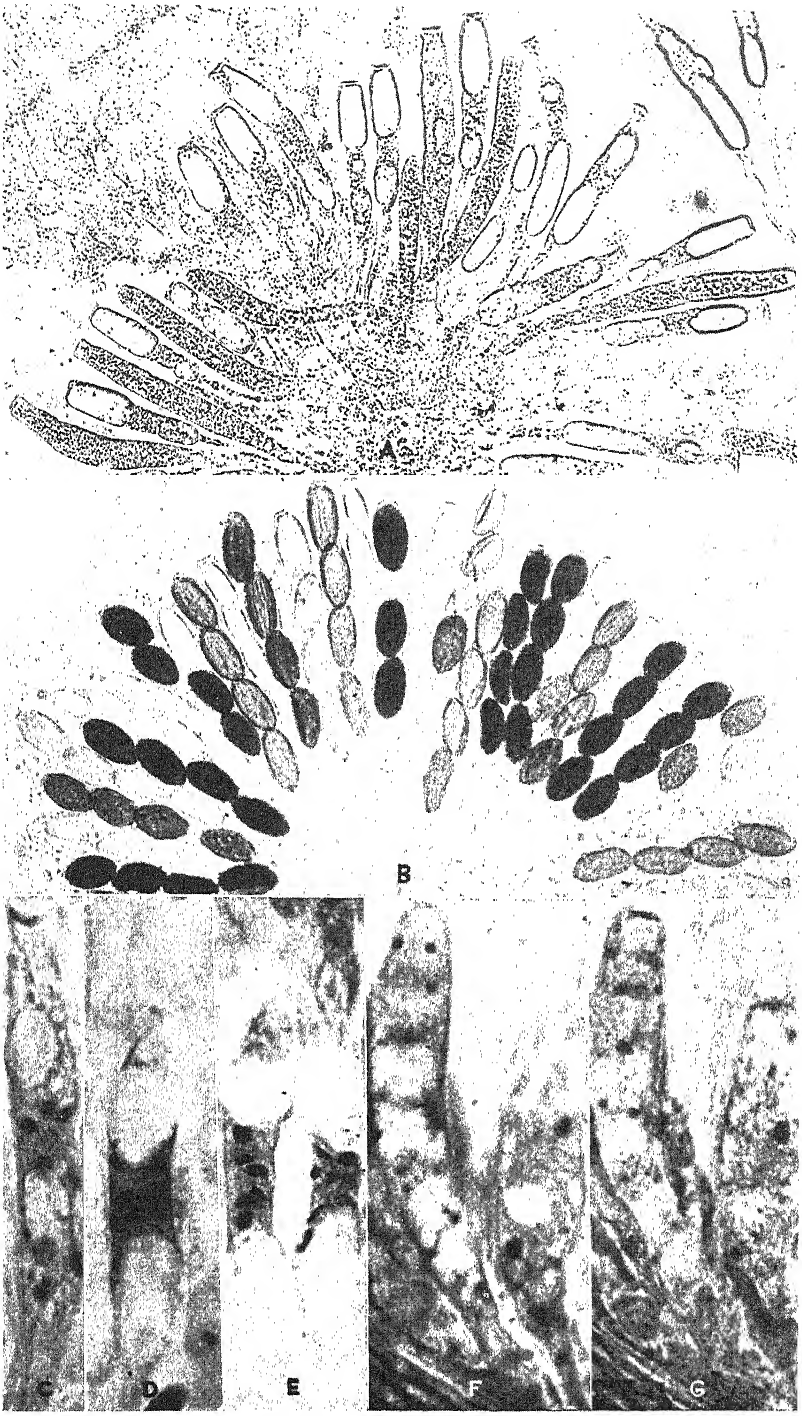
B. Asci heterozygous for the recessive factor l. Ascospores are delimited normally. Each spore will have originally two nuclei, one nucleus carrying l, the other nucleus of opposite sex and normal.

C–E. Photographs of stained preparations of four aborting asci homozygous for the recessive lethal l. (Compare with A above.) C, shows the eight nuclei after the third division separated into two groups by a vacuole. The vacuole in the upper end of this ascus looks like a hyaline spore. The string of cytoplasm connecting it with the tip of the ascus is not uncommon (See plate 9, C); D, E, three other asci in which the eight nuclei are crowded to the center where they are slowly degenerating. Some sections of perithecia show a dozen asci at this stage.

F, G. Two views of a section of an aborting ascus heterozygous for a lethal or deficiency due to irradiation of a parental ascospore. By focusing slightly one could see the sixteen nuclei resulting from a fourth precocious division. Their distribution and the foamy vacuolate cytoplasm are characteristic for the type of aborting asci shown in plate 9, A.



DODGE: NEUROSPORA



DODGE: NEUROSPORA

Studies in the Ericales

I. The genus Gaylussacia in North America north of Mexico

W. H. Camp[1]

In the western hemisphere, the genus *Gaylussacia* has become a depository for all the Vacciniaceae possessed of a 10-celled ovulary. This has brought together a group of plants which has but little in common in its several sections. Over forty years ago Drude[2] recognized three well defined sub-genera, namely:

(1) *Eu-Lussacia* Benth. and Hook.
(2) *Decachaena* T. and G.
(3) *Pseudo-Idaea* Dr.

In North America the species fall into the following divisions:

I. *Eu-Lussacia* Benth. and Hook. (*Lasiococcus* Small)
  G. mosieri (Small) Camp.
  G. orocola (Small) Camp.
  G. dumosa (Andr.) T. and G.
II. *Decachaena* T. and G. (*Decamerium* Nutt.)
  Sec. 1. Baccatae:
    G. baccata (Wang.) K. Koch.
  Sec. 2. Ursinae:
    G. ursina (M. A. Curtis) T. and G.
  Sec. 3. Frondosae:
    G. tomentosa (Pursh) Chapm.
    G. frondosa (L.) T. and G.
    G. nana (A. Gray) Small.
III. *Pseudo-Idaea* Drude (*Buxella* Small)
    G. brachycera (Michx.) A. Gray.

Although Small[3] has recently erected the genus *Lasiococcus* for *G. mosieri*, *G. orocola* and *G. dumosa*, the present writer is unwilling to accept the new genus until the forty or fifty species of the South American Gaylussacias are known in more detail.

For much the same reason the writer has not yet accepted Small's *Buxella*. It is to be admitted, however, that a rather cursory examination

[1] Papers from the Department of Botany, the Ohio State University, No. 332.
[2] Drude, O. Ericaceae in Pflanzenfamilien (Engler and Prantl) 4. pt. J: 49–51. 1891.
[3] Small, J. K. Manual of the Southeastern Flora. Pp. 1006–1009. 1933.

of various of the South American forms failed to locate any near relatives from which this monotypic section might have been derived.

Although it is possible that the genus Gaylussacia should be divided into three or four genera, the present writer will make no attempt to do so until more definite information of the group is at hand. Further, such a move at the present time would only be confusing to the student who would attempt to read the floristic and ecological literature of the southeastern United States where these species, under their present names, play so prominent a part.

The writer wishes to thank Mr. George Taylor of the British Museum for examining the type of *G. hirtella* (Ait.) Klotsch and also Dr. John K. Small of the New York Botanical Garden through whom the information was forwarded.

KEY TO THE SPECIES

1. Leaves evergreen, no glands on the lower surface of leaves. . .*G. brachycera* (Michx.) A. Gray. (Pa., E. Ky., E. Tenn., to Va., Md., and Del. Most abundant in SE W. Va.)

1. Leaves deciduous, glands present on the lower surface of the leaves. 2

 2. Glands on lower surface of leaves small, on generally curved, hair-like stalks. 3

 2. Glands on lower surface of leaves, large, short stalked and nearly sessile. 4

3. Hypanthium (receptacle, etc.) and fruit conspicuously bristly hairy with a dense cover of stalked glands. . . . .*G. mosieri* (Small) Camp. (Fla. to La.)

 The above is incorrectly known as *G. hirtella* (Ait.) Klotsch.

 G. orocola (Small) Camp. (*Lasiococcus orocola* Small) differing from the former in being less hairy, is known from one collection made near Flat Rock, N. Car. The specimen is in the Herb. N. Y. Bot. Gard., Bronx Park, N.Y.

3. Hypanthium and fruit with inconspicuous, stalked glands—*G. dumosa* (Andr.) T. and G. (Nfd., to Fla., and La.)

 Var. *Bigeloviana* Fernald differs from the species in having the glands on the upper surface of the leaf somewhat more persistent. Mingled with the species from Nfd., southward—doubtfully distinct south of Mass., or N. J.

 4. Resin glands present and generally abundant on both surfaces of the leaf: (fruit black). . . . .*G. baccata* (Wang.) K. Koch (Nfd., to Man., and Sask., south to Iowa, Ky., and Georgia)

 Forma *glaucocarpa* (Robinson) Mackenzie with glaucous blue fruits, sporadic, Me., to N. Car.

 Forma *leucocarpa* (Porter) Fernald with white or pinkish, translucent fruits, sporadic, throughout the range of the species.

 4. Resin glands present on lower surface only of the leaf. 5

5. Leaves with both surfaces tomentose, particularly so beneath, tomentum brown or gray, leaves leathery. . . . .*G. tomentosa* (Pursh) Chapm. (Ga., Fla. and Ala.)

5. Leaves glabrescent or sometimes pubescent, hairs more or less silvery, leaves green or glaucous, thin or sometimes leathery. 6

 6. Leaf apex short acuminate and markedly apiculate; stamen filaments pubescent. . . . .*G. ursina* (Curtis) T. and G (Deep forests of the Unaka Range and its outliers in the Carolinas, Tenn., and Ga.)

6. Leaf apex generally notched and revolute, occasionally acute and minutely apiculate; stamen filaments glabrous 7
7. Mature leaves green or pale and if glaucescent, on the lower surface only 8
7. Mature leaves with both surfaces markedly glaucescent 9
8. Inflorescence bracts small, oblong or linear, generally deciduous . . *G. frondosa* (L.) T. and G. (N. H., to Fla., and La., not present outside the Atlantic and immediate Gulf Coast drainages, erroneously reported from Ohio)
8. Inflorescence bracts large and often leaf-like, ovate to ovate-spatulate, often persistent . . . . *G. frondosa* var. *polycodioides* Camp. (Coastal region, N. J. and Mass.)
9. Plants low, 1–4 dm.; leaves 2–3 cm. long . . . . *G. nana* (A. Gray) Small. (Ga., Fla., and Ala.)
9. Plants higher, 4–10 dm.; leaves 2.5–7 cm. long . . . . *G. frondosa* forma *glaucophylla* Camp. (Sandy areas along the coast, Mass., to N. Car.)

Gaylussacia frondosa var. polycodioides var. nov.

Shrub .5–1.5 m. tall, branchlets sparsely pubescent. Mature leaves firm-membranaceous, 3–7 cm. long, 1.5–3.5 cm. wide, upper surface light green and generally glabrous except for the sparsely pubescent mid-vein; lower surface pale, glaucescent, sparsely pubescent, glandular, the margin somewhat revolute. Fruiting panicles 4–7 cm. long; *bracts semipersistent, 8–24 mm. long, 3–10 mm. wide, ovate to ovate-spatulate, subobtuse to acuminate.* Fruit frosty blue, semiglobose, 5–8 mm. in diameter, pedicels 10–18 mm. long. Flowers unknown.

Frutex 0.5–1.5 m. altus ramulis sparse pubescentibus; folia matura firme membranacea 3–7 cm. longa 1.5–3.5 cm. lata, supra pallide viridia et glabra, costa centrali sparse pubescente excepta, subtus pallida glaucescentia glandulosa, margine paullo revoluto; paniculae fructiferae 4–7 cm. longae; bracteae sub-persistentes 8–24 mm. longae 3–10 mm. latae ex ovatis ovato-spatulatae, ex subobtusis acuminatae; fructus glauco-coeruleus semiglobosus 5–8 mm. diametro, pedicellis 10–18 mm. longis; flores ignoti.

This variety, although known from only three localities, obviously belongs with *G. frondosa* but may easily be distinguished from the species by the large, leaf-like, and generally persistent bracts. The writer has chosen the name (*polycodioides*) because of the marked resemblance of the plant in the field to the deerberries (*Polycodium*). It may be easily differentiated from the associated form (*Polycodium stamineum*) by the presence of the large glands on the lower surface of the leaves.

Type locality: On the margin of a *Chamaecyparis* bog, one-half mile south of Toms River, New Jersey.

The type specimen will be deposited in the Herbarium of the New York Botanical Garden, Bronx Park, N. Y., and a co-type in the Gray Herbarium, Cambridge, Mass.

Other collections: (1) In a "Cedar swamp" near Falmouth, Barnstable Co., Mass., Sept. 24, 1915. E. Dean, A. J. Eames and L. H. MacDaniels.

Herb. Dept. of Bot., N. Y. State Coll. of Agri., Ithaca, N. Y. (2) West Tisbury, Martha's Vineyard, Mass., June 30, 1916. F. C. Seymour. Gray Herbarium, Cambridge, Mass.

Gaylussacia frondosa forma **glaucophylla** forma nov.

Shrub 4–10 dm. tall, *branchlets glaucescent.* Mature leaves firm-membranaceous to rugose, 2.5–7 cm. long, 1.3–3.5 cm. wide, *upper surface greenish-glaucescent*, often markedly so, lower surface pale glaucescent.

Frutex 4–10 dm. altus ramulis glaucescentibus; folia matura ex firme membranaceis rugosa, 2.5–7 cm. longa 1.3–3.5 cm. lata, supra viridi-glaucescentia, saepe conspicue sic, subtus pallide glaucescentia.

This form may be found in many herbaria with the species but the locality and habitat labels indicate that it is found in sandy areas close to the coast from Massachusetts to North Carolina and southward where it perhaps grades into *G. nana* (A. Gray) Small. In the mid-atlantic states, however, it may be distinguished from *G. nana* by its larger leaves and from *G. frondosa* by its highly glaucescent twigs and leaves.

SUMMARY OF NEW COMBINATIONS AND VARIETIES

Gaylussacia mosieri (Small) Camp. (*Lasiococcus mosieri* Small)
Gaylussacia orocola (Small) Camp. (*Lasiococcus orocola* Small)
Gaylussacia frondosa var. *polycodioides* Camp.
Gaylussacia frondosa forma *glaucophylla* Camp.

A study of chromosome pairing in Yucca rupicola

G. M. WATKINS

(WITH PLATES 11 AND 12)

INTRODUCTION

The pioneer work of van Beneden (1883) on *Ascaris megalocephala* showed for the first time that each parental nucleus contributes one basic complement of chromatin to the zygote nucleus. Overton (1893) showed that the number of chromosomes in nuclei of both male and female gametophytes of *Ceratozamia mexicana* is eight, and that double this number are found in sporophytic nuclei. In a number of other species the same relation was observed between chromosome numbers in gametophytic and sporophytic tissue. These discoveries supplemented those of Hofmeister very remarkably. Their importance was immediately recognized, and later investigators have considered from various standpoints the problem of the interrelationships of the haploid and diploid chromosome sets in the gametophytic and sporophytic phases of the life cycle. The idea of chromosome homology proposed by Montgomery (1901, 1905) and Sutton (1902) further developed the concepts in this field and gave impetus to the belief that the chromosomes which pair at the time of synapsis are really corresponding homologous members of separate gametic complements.

The work of Strasburger (1905) and the corroborative studies of many subsequent investigators have proved that the pairing of chromosomes during divisions of somatic nuclei in many plant species is a tangible reality. In *Yucca* its presence was early demonstrated by Müller (1909) in root tip nuclei in three species. In the present study I have been able to confirm the observations of Müller, and further to show that the paired relation of chromosomes is a general one which applies to all somatic cells in the adult plant. In my preparations of *Y. rupicola* pairing is completed by the time the chromosomes appear upon the equatorial plate of the first zygotic mitosis.

LITERATURE REVIEW

Montgomery's (1901) conception that each chromosome of one parental complex has its structural and physiological counterpart within the other complex was based upon his studies of division figures in diploid nuclei in which marked size differences occur among the chromosomes. He observed that in such cases there are two chromosomes of each given size, and though these two do not always appear in juxtaposition to each

other, he showed that the members of each structurally similar pair come together and fuse at the time of division of the gonotokont nuclei. Sutton (1902) found in the diploid nuclei of *Brachystola* that, although the chromosomes are not actually placed in pairs, he could arrange them in a series of pairs based on size differences. He thus observed that there are two chromosomes in each size category. A later paper by Montgomery (1905) described a partial pairing of the chromosomes of *Syrbula* in the last spermatogonial divisions.

Further progress in the development of the concept of chromosome pairing resulted from the extensive investigations of Strasburger (1905, 1907, 1909, 1910) upon various species of plants. In mitosis in root tips of *Funkia sieboldiana* and *Galtonia candicans* he observed striking size differences among the chromosomes, and that chromosomes of like size tend to pair during mitosis. He believed that the paired arrangement of homologous chromosomes is a widespread phenomenon in plants.

These researches initiated a long series of studies by other investigators on the question of chromosome pairing in somatic nuclei, and pairing was accordingly described in a wide range of plant species of many different families and orders. These data are presented in Table 1, which gives a list of plant species in which such pairing has been reported.

Clemens Müller (1909), working in Strasburger's laboratory, studied mitosis in root tips of three species of Yucca (*Y. aloifolia*, *Y. draconis*, and *Y. guatemalensis*). According to his account the three species are cytologically identical and are characterized by the presence in diploid nuclei of ten long, club-shaped chromosomes and about forty-four to forty-six which are very small and almost spherical. The large chromosomes are almost always arranged in five pairs, and the small ones also tend to pair. Müller followed the progress of the chromosomes in root tip cells from their first emergence out of the resting nuclear reticulum through all the phases of mitosis until their final disappearance in the late telophases. In every phase where the chromosomes are clearly visible they are arranged in pairs. Müller's contentions are well supported by excellent photographs of his preparations as well as numerous drawings.

Shortly afterward Bonnet (1911) contradicted Müller's views, stating that in somatic divisions of *Yucca* the chromosomes are not paired, and that any such appearance is due entirely to a fortuitous side-by-side arrangement. In my opinion Bonnet's criticism, which was based on his observations of mitosis in *Y. gloriosa*, carries no great weight, since his material was so poorly fixed that the chromosomes appear as little more than a fused chromatin network lying in the equatorial plane.

Müller further substantiated his views in a second paper (1912) dealing

TABLE 1

SPECIES	FAMILY	AUTHORITY
Morus indica	Moraceae	Tahara, 1910
Cannabis sativa	Moraceae	Strasburger, 1910
Spinacia oleracea	Chenopodiaceae	Stomps, 1910
Lychnis dioica	Caryophyllaceae	Sykes, 1908
Pisum sativum	Leguminosae	Strasburger, 1907
Mercurialis annua	Euphorbiaceae	Strasburger, 1910
Ricinus zanzibariensis	Euphorbiaceae	Nemec, 1910
Mouriria anomala	Melastomataceae	Ruys, 1924, 1925
Nicandra physaloides (paired prochromosomes)	Solanaceae	Janaki-Ammal, 1932
Plantago lanceolata	Plantaginaceae	Nemec, 1910
Bryonia dioica	Cucurbitaceae	Sykes, 1908
Dahlia spp.	Compositae	Ishikawa, 1911 Lawrence, 1929
Naias marina	Naiadaceae	Müller, 1912
Hydrocharis morsus-ranae	Hydrocharitaceae	Sykes, 1908
Bulbine annua	Liliaceae	Müller, 1912
Funkia sieboldiana	Liliaceae	Strasburger, 1905 Sykes, 1908 Müller, 1912
Funkia ovata	Liliaceae	Sykes, 1908
Aloë hanburyana	Liliaceae	Müller, 1912
Albuca fastigiata	Liliaceae	Müller, 1912
Galtonia candicans	Liliaceae	Strasburger, 1905 Sykes, 1908 Müller, 1912
Eucomis bicolor	Liliaceae	Müller, 1912
Muscari botryoides	Liliaceae	Müller, 1912
Scilla bifolia	Liliaceae	Müller, 1912
Chionodoxa lucillae	Liliaceae	Müller, 1912
Hyacinthus orientalis	Liliaceae	Müller, 1912
Yucca aloifolia	Liliaceae	Müller, 1909, 1912
Yucca draconis	Liliaceae	Müller, 1909, 1912
Yucca guatemalensis	Liliaceae	Müller, 1909, 1912
Beschorneria superba	Amaryllidaceae	Müller, 1912
Nerine rosea	Amaryllidaceae	Müller, 1912
Oryza sativa	Gramineae	Kuwada, 1910
Holcus halepensis	Gramineae	Huskins and Smith, 1932
Listera ovata	Orchidaceae	Müller, 1912

Table 1—Plants in which pairing of chromosomes in divisions of somatic nuclei has been reported.

with chromosome arrangement in fourteen genera of the Liliaceae, Amaryllidaceae, Orchidaceae, and Naiadaceae (see table 1). In all of the plants studied he demonstrated a definite tendency for the chromosomes to pair in diploid mitoses.

Additions to the data relating to chromosome pairing were made

by Tahara (1910) on *Morus indica*, Kuwada (1910) on *Oryza sativa*, and Ishikawa (1911) for various species of *Dahlia*. In these cases the chromosomes were said to be paired in somatic mitoses and also in the homoeotypic divisions of microsporogenesis. Ishikawa offered the explanation that these forms are really tetraploid in the sporophytic generation and that the reduced number of chromosomes found in the homoeotypic divisions and in the gametophytic nuclei nonetheless contains two basic complements. Hence, any tendency toward pairing of homologues can well be expressed even in homoeotypic divisions. This peculair type of chromosome arrangement, to which Darlington (1928) has applied the term "secondary pairing," has also been figured and described for *Mercurialis annua* by Yampolsky (1925).

The work of Montgomery (1901) and Sutton (1902) provided the stimulus for a series of investigations on the occurrence of chromosome pairing in non-meiotic divisions in animal cells. Miss Stevens (1908) described chromosome pairing for all spermatogonial divisions of *Culex*. Her observations were substantiated by Metz (1914, 1916) in a series of studies on chromosomes in approximately eighty species of the Diptera. The association in distinct pairs of the homologues in various somatic and spermatogonial nuclei of the flies, as described by Metz, is perhaps the most perfect and diagrammatic so far reported for any organism. As a rule the Diptera seem to have comparatively low chromosome numbers and also to combine several size categories for each species, and the phenomena described by him appear to be general for the entire order.

Metz and Nonidez (1921, 1923) described spermatogonial and meiotic divisions in *Asilus sericeus* and *A. notatus*. In the last spermatogonial division of *Asilus*, according to their description and figures, the pairing of the homologous chromosomes in the telophases is so intimate that it takes the place of synapsis. No leptotene stage is present in the meiotic prophases and the chromosomes appear immediately as greatly condensed bivalents. A similar condition was observed in *Dasyllis grossa* (Metz, 1922b). Whiting (1917) described conditions for *Culex* which agree essentially with those figured by Metz for the order as a whole.

Robertson (1930), studying chromosomes of both parthenogenetically produced and biparental individuals of *Apotettix eurycephalus* and *Paratettix texanus*, found that in dividing nuclei of the former class, the chromosomes are closely paired, but in biparental individuals the chromosomes of the gametic sets appear on opposite sides of the spindle. He suggests that the partheno-produced individuals may have arisen from the type of egg which has a single pronucleus containing seven double or diad-like chromosomes, and that the biparental form comes from an egg with two

pronuclei, each of which contains seven single or monad-like chromomoses. This would account for the appearance of the same chromosome numbers in both types, and it is offered by Robertson as an explanation for the interesting variation from chromosome pairing to gonomery within the same species.

As a corollary to his idea that homologous chromosomes tend to pair in diploid somatic nuclei Strasburger (1907) suggested that in polyploid nuclei the chromosomes might be found aggregated in still larger groups than pairs. He investigated dividing nuclei in endosperm tissue, which is triploid, and analyzed syndiploid nuclei of chloralized pea root tips to to determine whether groups of four are present. He never observed these, however, and concluded that the affinity which homologous chromosomes have for each other is satisfied when two homologues pair, and that no tendency to form larger groups is present. Strasburger's figures of equatorial plates of syndiploid pea root tip nuclei show a pronounced pairing, but no evidence of grouping in fours.

This aspect of the problem has received little further study and the data available do not warrant generalizations. Ruys (1924, 1925), on the other hand, has figured two division stages of endosperm nuclei in *Mouriria anomala* which showed the chromosomes arranged in groups of three. The haploid number in this species is twelve, and Ruys observed in the metaphase figure twelve groups of three chromosomes each. In diploid equatorial plate figures in nucellar tissue he observed twelve pairs. Metz (1922a) reported divisions of certain tetraploid somatic nuclei in *Sarcophaga*, a dipteran, in which the haploid number is six, and division figures are given showing six groups of four chromosomes each. Miss Holt (1917) described various complex nuclei in *Culex;* these ranged from diploid to polyploids with twenty-four basic sets of three chromosomes per set. In the less complicated polyploid nuclei her figures show the homologues grouped together, but in the higher polyploids the association is not realized.

The data accumulated since 1905 are sufficient to indicate strongly that the phenomenon of chromosome pairing in nuclei of somatic tissue is clearly defined and tangible for a large number of plant species as well as for at least one order of animals. Almost all data, however, relate to cells in isolated embryonic zones in the more or less mature organism. These cells are many mitotic generations removed from the point of initiation of the diploid state, and hence they throw no light on the time and manner of origin of the paired condition. In his various papers Metz has shown that the chromosomes are paired in the cells of very young dipteran larvae, but even these stages are far later in development than the point where

the relationship might possibly begin. Huettner (1923), in a study of the origin of germ cells in *Drosophila melanogaster*, found that after fertilization the nuclei during the fifth, sixth, and seventh cleavage stages are located at the end of the egg in a zone of granular polar cytoplasm. During these nuclear divisions Huettner observed that the chromosomes are paired. In a later paper (1924) he showed that at syngamy in the same organism the male and female pronuclei approach each other in the resting condition and without fusing proceed to the formation of gonomeric spindles side by side. Homologous chromosomes do not mingle, and pairing of the homologues occurs for the first time in the second cleavage.

According to the account given by Hutchinson (1915) for fertilization and division of the zygote nucleus in *Abies balsamea*, the egg and sperm nuclei fuse in the resting condition. Following this two groups of chromosomes arise in the micropylar end of the fusion nucleus, and as the first division spindle is set up the two groups become intermingled at the equatorial plate with the chromosomes arranged in pairs. Each pair undergoes transverse segmentation and the daughter segments, still paired, go to opposite poles and the daughter nuclei are reconstructed. A similar process was described by Chamberlain (1916) for fertilization in the cycad, *Stangeria paradoxa*, and by Miss Weniger (1918) for *Lilium philadelphicum* and *L. longiflorum*. These three accounts have been criticized by Sax (1918), because the reported transverse segmentation of the chromosomes is not in line with the more widely accepted conceptions of the manner of distribution of the daughter chromatin elements in mitosis.

The published data relating to the pairing of chromosomes in somatic cells of *Yucca* are limited to the papers of Clemens Müller (1909, 1912) and Bonnet (1911) previously mentioned. Other cytological details, as presented by various authors for a number of species of the Yucceae, are listed in table 2.

MATERIALS AND METHODS

I have studied especially *Yucca rupicola* Scheele. Cytological material was collected in the field at Austin, Texas, during flowering time through three successive summers. Preliminary fixations were made in a variety of solutions, and from a study of these the Allen and Wilson modification of Bouin's solution was selected for the preservation of large numbers of young flowering buds, slices of developing ovaries after pollination, and young ovules in various stages of development. Seeds were germinated in sand and between sheets of moist filter paper, and when the seedling roots were from one to three centimeters long the tips were removed, rinsed

briefly in the case of those grown in sand, and fixed in the modified Bouin's solution. All material was imbedded in paraffin, sectioned at varying thicknesses from 7 to 15 microns, and stained with the Flemming triple stain or by the Heidenhain iron alum-haematoxylin method.

TABLE 2

SPECIES	CHROMOSOME NUMBERS N	2N	AUTHORITY
Hesperaloë parviflora	30	—	McKelvey and Sax, 1933
Hesperoyucca whipplei	30	—	McKelvey and Sax, 1933
Samuela faxoniana	30	—	McKelvey and Sax, 1933
Yucca aloifolia	—	54–56	Müller, 1909, 1912
Y. angustissima	30	—	McKelvey and Sax, 1933
Y. constricta	30	—	McKelvey and Sax, 1933
Y. draconis	—	54–56	Müller, 1909, 1912
Y. elata	30	—	McKelvey and Sax, 1933
Y. filamentosa	—	—	Koernicke, 1901
	—	—	Taylor, 1925
	30	—	Morinaga, *et al.*, 1929
	30	—	McKelvey and Sax, 1933
Y. flaccida	30	—	O'Mara, 1931
	30	—	McKelvey and Sax, 1933
Y. glauca	6	12	Folsom, 1916
Y. gloriosa	—	—	Bonnet, 1911
Y. guatemalensis	—	54–56	Müller, 1909, 1912
Y. macrocarpa	30	—	McKelvey and Sax, 1933
Y. recurva	ca. 25	54–56	Woycicki, 1911, 1925
Y. rupicola	30	—	McKelvey and Sax, 1933

Table 2—Chromosome studies in the Yucceae.

OBSERVATIONS

Mitosis in root tips

Resting nuclei in the root tips usually show a single nucleolus surrounded by a very finely drawn chromatic reticulum. In many cases a clear space lies between the nucleolus and the chromatin, a characteristic which is shown in the photographs by Müller (1909). As the prophases begin the chromatin becomes aggregated into densely staining discrete chromosomes which show no evidence of forming a continuous spireme. At this stage it becomes apparent that there are two sizes of chromosomes, one group of long, rod-like chromosomes and another of short, almost spherical ones. Chromosomes of both sizes are completely intermingled and show no specific plan of orientation. At this stage definite pairs of chromosomes are seldom visible.

As the nuclear membrane breaks down and the nucleolus disappears the central spindle is formed with the chromosomes distributed across the plane of the equatorial plate. The distribution of these chromosomes corresponds closely with previously published accounts (e.g., Strasburger, 1905; Miyake, 1905; and Müller, 1909, 1912) of equatorial plate figures in species which have chromosomes of markedly different sizes. That is, the small ones occupy the central area and the large chromosomes radiate out peripherally from the margin of the spindle. In figures 1, 2, and 3 are shown polar views of such equatorial plates. Careful counts of a large number of plates indicate that there are ten large chromosomes and fifty small ones. The typical radial placement of the long chromosomes may be varied occasionally by the vertical orientation of one or more pairs. The reason for these exceptions is not apparent, but it is to be noted that the spindle fiber attachments of all the long members are terminal, and that the distal portions of the chromosomes are free to become oriented by other agencies than the spindle fibers themselves. In other words, each long member of the chromosome complex appears to pivot about a locus established by the spindle attachment.

In the majority of equatorial plate stages examined a marked tendency toward pairing of the chromosomes is evident. Figures 1, 2, and 3 are typical of the condition described. With the view of emphasizing more objectively the long chromosomes which appear to constitute a pair they have been indicated alphabetically in these figures. The pairing is not sufficiently intimate and close to suggest synaptic pairing or chromosome conjugation in meiosis, but it is, nevertheless, easy in most cases to recognize for each long chromosome a definite partner or mate, not only because of similarity in size and shape, but also through its close proximity and similarity in direction of orientation. Pairing is also evident in a large number of small chromosomes, but their great number and close crowding render the relationship less obvious than in the former group. Contrary to the findings of Müller for *Y. aloifolia*, *Y. draconis*, and *Y. guatemalensis*, I have been able to demonstrate pairing clearly in only the equatorial plate stages of root tip mitoses. His figures show pairing through mitosis from the prophases to the telophase condition. In figure 4 is shown an anaphase typical of root tip mitoses in *Y. rupicola*. Doubtless the tendency to pair is here just as strong as in the equatorial plate, but because of the crowding of the chromosomes as they approach the poles, it is more difficult to recognize. At the stage shown in figure 4 the small chromosomes may often be so crowded as to make identification of the individuals impossible. Nevertheless the long chromosomes in this anaphase figure are arranged in fairly definite pairs.

Mitosis in ovarian tissue

In the walls of young ovaries nuclear division is fairly frequent and various stages of mitosis can readily be observed. A careful study of these stages shows them to be similar in every detail to the corresponding processes in root tips. In equatorial plate stages the long chromosomes are paired and are radially placed, with the small ones in the central part of the figure. Pairing is conspicuous, especially among the long chromosomes, in most nuclei at this stage, as is shown in figures 5 and 6. Prophases and telophases failed to show consistent evidence of chromosome pairing, possibly due again to the difficulty of analyzing the relationships existent within them.

Mitosis in young embryos

Despite the very great difficulty involved in the location of clear equatorial plate figures in young embryos of *Yucca*, a sufficient number of mitoses have been found in the early embryonic stages to give a clear picture of the arrangement of the chromosomes during this part of the sporophytic development. In figure 7 is shown a polar view of an equatorial plate which is typical of several such stages observed in an embryo containing probably between five hundred and a thousand cells. Many of the smaller chromosomes are omitted from this drawing, due to their overlapping and the consequent difficulty in determining their exact number and positions. The large chromosomes lie in their characteristic positions and are definitely paired. A younger embryo is shown in figure 12. It contains a filament of five cells, the central one of which contains an equatorial plate stage. This figure, although seen in profile view, is so clear that it is easily possible to follow the exact positions of the long chromosomes, and to reconstruct from it an orthographic projection showing the appearance of the plate from the apical pole, as illustrated in figure 11. Figure 13 is an enlarged camera lucida drawing of the original mitotic figure. Here is a clear cut case of pairing of the long chromosomes. Pairs "*a*", "*b*", "*c*", and "*d*" show the typical radial arrangement previously described, while pair "*e*" lies in the vertical direction at right angles to the equatorial plate.

The evidence as to the pairing of the chromosomes during the early prophases of mitosis in these filamentous embryos is so far indecisive, because of the limited number of such stages found. Several prophases have been studied in which the chromosomes appeared thoroughly intermingled and with no obvious paired arrangement. A few figures were found, however, in which several chromatic units were seen lying side by

side, as is shown in figure 10. The paired arrangement of the chromatin rods in this figure indicates that pairing is achieved in the late prophases, but it is not certain at what stage in mitosis it becomes conspicuous.

In figure 8 is shown an oblique view of an equatorial plate from an embryo in the three- or four-celled stage. All of the long chromosomes can be seen clearly and they are definitely assorted in pairs. The embryo shown in figure 9 consists of three cells, the apical of which is in the telophase of mitosis. Reorganization of the daughter nuclei has proceeded to a considerable extent and the chromosomes have become almost completely transformed into a characteristic interkinetic reticulum.

A series of stages showing some of the steps in mitosis in the first division of the fertilized egg or one-celled embryo are illustrated in figures 14, 15, 16, and 17. Unfortunately the embryo shown in figure 14 was cut through by the knife, but, since the chromosomes appear to be undisturbed, it was deemed worth while to draw separately each part of the embryo as it appeared in the serial sections. The prophase chromosomes appear as discrete, thickened bodies in this stage. Although there seems to be sufficient space in the nucleus to allow the chromosomes to assume almost any grouping, they are irregularly distributed and no pairing is evident.

Figure 15 shows an equatorial plate of the first embryonic mitosis. This figure is unusual in that it shows three of the five pairs of chromosomes oriented vertically, leaving only two pairs lying in what has been postulated as the typical radial orientation. Of these latter two pairs one is shown heavily shaded (pair "*a*") and extends obliquely upward from the spindle. The other radially disposed pair cannot be indicated in this drawing, due to the fact that it extends straight downward beneath the mass of small chromosomes. The pair can be accurately determined in the preparation by focusing slowly downward. The paired arrangement of the large chromosomes in this figure is clear and well defined.

A slightly later stage is shown in figure 16. This is a very early anaphase stage and shows the chromosomes just after separation of the daughter halves. The long chromosomes are still pointed outward and poleward much as they are on the equatorial plate, and the distal portions have not yet manifested the lagging equatorial orientation which characterizes them in later anaphases. Pairing of the chromosomes is not conspicuous in this figure. In a somewhat more advanced anaphase, such as the one shown in figure 17, the long chromosomes are trailing behind the general group as the poleward movement proceeds. In this figure there is some evidence of pairing.

The shape of the achromatic figure becomes much changed as the

anaphase occurs. At the equatorial plate stage (fig. 15) the spindle is fairly broad and the fibers become indistinct before converging at the poles. The same applies to the early anaphase (fig. 16). But during later anaphases the spindle becomes extended longitudinally and the fibers converge into sharp, distinct points at the poles (fig. 17).

Nuclear division in the endosperm

In addition to the observations described above a study was also made of the free nuclear divisions which occur during the early development of the endosperm, with the purpose of determining whether the same affinity of homologous chromosomes found in diploid nuclei is manifested also in the endosperm, which presumably is triploid. In view of the fact that the triple fusion of a sperm cell with the two polar nuclei has so far not been observed in *Yucca*, it is not certain that the endosperm nuclei studied have arisen in the normal manner. Chromosome counts in the endosperm have yet failed to show the theoretical triploid number, i.e., ninety, but a number of figures have been studied in which about seventy-five chromosomes were recognizable. Perfect nuclear fixation is an absolute requirement for the accurate study of nuclei with such high chromosome numbers, and this is obtained only with the greatest difficulty in the endosperm, which is surrounded by many layers of cells.

Figures 18 and 19 show typical late prophases from the endosperm. No definite arrangement of the chromosomes in groups of three is visible in these nuclei, and the same irregular intermingling of chromosomes is evident in the equatorial plate stages of figures 20 and 21. There is here no visible tendency of the chromosomes to be arranged in groups of three. These observations are perhaps in accord with the assumption of Strasburger that when two chromosomes pair their mutual affinities are satisfied and there is no further tendency toward the formation of larger aggregations. In endosperm nuclei there is little or no evidence at hand that the homologues are arranged in any specific manner with reference to each other. In general, as shown in figure 21, the long chromosomes tend to radiate out from the margin of the chromosome group with the small chromosomes occupying the center.

In a recent study of chromosomes in the hemipter, *Archimerus alternatus*, Wilson (1932) has described the preservation of a so-called stable metaphase pattern in haploid, diploid, and tetraploid nuclear divisions. Regardless of the number of basic chromosome complexes present the autosomes tend to form a ring, with the small m-chromosomes in the center and the x-chromosomes on the outside. This is considered evidence for the view that each chromosome, together with its allotment of achromatic

material, is an autonomous unit within the nucleus, which takes a specified position upon the spindle regardless of additional complications such as the reduplication of chromosome complexes. The view that there is a permanently fixed relation between the chromosomes and the achromatic material was early presented by Rabl (1885) for animal nuclei and by Harper (1896, 1905) in his work on nuclear division in *Erysiphe* and *Phyllactinia*. Bleier (1930) has recently subscribed to this view in connection with his discovery of a type of gonomery in meitoic divisions in pollen mother cells of *Triticum* x *Secale* and *Aegilops* x *Triticum* hybrids. Bleier's term for this feature is "Krypto-gonomerie," and he employs the term "paragenoplast" for the allotment of achromatic material which goes with each chromosome.

Yucca also preserves the same equatorial plate pattern in haploid, diploid, and possibly triploid mitoses; the large chromosomes are radially placed at the periphery of the figure, while the small ones occupy the central position. Haploid figures conforming to this scheme have been presented by Morinaga *et al.* (1929), O'Mara (1931), and McKelvey and Sax (1933), diploid figures by Müller (1909), and both diploid and triploid are here presented in figures 1, 2, 3, 5, 6, 7, 8, 11, 20, and 21.

DISCUSSION

In the majority of papers dealing with the subject of chromosome pairing in diploid nuclei the basic assumption is that the members of each pair are derived from the paternal and maternal parents respectively. Montgomery's contribution was primarily a suggestion of the homology of chromosomes which fitted admirably with the facts at hand, and the strength of that suggestion is attested by the fact that it is still applicable to the data accumulated in the three decades since its proposal. However, the organisms which he studied showed chromosome pairing only at synapsis or during the last spermatogonial division, thus leaving a gap of many cell generations during which visible evidence of the homology had not been traced. Strasburger and his students narrowed the gap considerably by their studies of species which show chromosome pairing in diploid somatic nuclei, root tips chiefly, but these data do not include the processes of syngamy or the early stages in the development of the sporophyte. Müller's excellent work on *Yucca* refers to karyokinesis in root tips, and his conclusive evidence of chromosome pairing in such nuclei was not only strong support for the theory of chromosome individuality, but also substantial correlative evidence that the members of each pair are homologous.

My data are further and more conclusive visible evidence of this

homology, since it has been shown that in *Yucca* the chromosomes occur in pairs in diploid somatic nuclei in various parts of the plant, and in young developmental as well as in more mature stages. The chromosomes, according to my observations so far, first appear in pairs upon the equatorial plate of the first zygotic division spindle and continue thus throughout the development of the sporophyte. Further data as to chromosome homology may come from a careful serial study of gametic karyogamy to determine when and how the assortative matings of the chromosomes come about.

The work of Huettner (1924) offers to the solution of this problem perhaps the most specific data to be found among the investigations in animal cytology, since he has demonstrated that in *Drosophila melanogaster* the beginning of the paired relationship takes place sometime in the interphase between the telophases of the first gonomeric cleavage division and the metaphases of the second divisions, where the chromosomes are first seen in pairs.

In comparing diploid equatorial plates of *Yucca* with those of other organisms in which pairing of chromosomes in somatic divisions has been described, striking differences in the intimacy of the association are at once noted. These may perhaps be due to variations in affinity between the members of the different pairs. In general it may be said that the intimacy of the pairing is more evident as described in the Diptera than in most of the plants studied. Heitz and Bauer (1933) and Painter (1934) have recently reported synapsis in somatic nuclei in certain species in this order. Heitz and Bauer found typical synapsis figures in cells of ovarian follicles and the malpighian vessels in *Bibio hortulanus*, and Painter has described a similar chromosome conjugation in the salivary glands of larvae of *Drosophila melanogaster*. Additional evidence of the close relationship between homologues in the Diptera is seen in the tendency of the chromosomes to aggregate in larger groups than pairs in the higher polyploids. As previously mentioned the presence of larger aggregates is as yet not well authenticated for plants.

As Miss Fraser (1912) has pointed out, the various groups of organisms may differ widely with respect to the behavior of gametic chromatin after fertilization. On this basis it is possible to arrange some of the known cases of fertilization in a series based on the rapidity with which parental chromosomes become associated together and also upon the closeness of this association. First in this series, so far as known, is *Yucca*, since pairing of homologous chromosomes occurs by the time they appear upon the equatorial plate of the first zygotic division. Close to *Yucca* would come *Drosophila melanogaster*, for Huettner's (1924) account has shown that

the paired relationship begins with the second embryonic mitoses. Next in the series would come the several plant species, such as *Pisum sativum*, *Mouriria anomala*, and *Galtonia candicans*, which show a pairing of chromosomes in somatic divisions, but in which the pairing has so far been demonstrated only in the adult plant. In none of these forms has the pairing in somatic nuclei been adequately shown to preclude the existence of synaptic pairing. The next group in order is the large class into which nearly all plant and animal species fall, as judged by the literature. In these there is complete karyogamy at the time of fertilization, but no obvious pairing of parental chromatin units until near the end of the diploid phase, that is, during meiosis. A further departure is found in *Pinus* (Ferguson, 1904), which behaves in the same manner as the last group except for the manifestation of gonomery in the first division of the sporophyte. The cases of *Cyclops* (Rückert, 1895; Häcker, 1895) and *Cryptobranchus* (Smith, 1919) are still farther removed, because in them the condition of gonomery persists for a varying number of cell generations after fertilization.

As the other extreme in this series we find the condition existing in the rusts and some other groups of fungi. In the rusts fertilization seems to consist of a type of plasmogamy which is not accompanied by karyogamy. As this diploid phase progresses the two gametic nuclei are found closely associated as a dikaryon. They undergo conjugate nuclear divisions for a period until the teleutospore stage is reached. Then nuclear fusion occurs, only to be followed immediately by meiosis and a return to the haploid condition. Far from the state found in *Yucca* these rusts seem to show entire independence of the parental chromosomes throughout almost the entire diploid phase of the life cycle.

Winge (1917) has recognized the problem of the varying behavior of gametic chromatin following syngamy in different organisms, and has attempted to classify and label from this standpoint three types of gametic activity. His term "philozygoty" refers to the union of gametes which are in complete harmony with each other, such as gametes from the same species. The harmony may be such as to result in pairing of chromosomes, although Winge states that this is often first visible in the sporogenous cells. By definition the application of the word "philozygoty" is too vague to be useful for distinguishing members of the series which has been postulated above, because all the forms listed, even with their widely varying degrees of gametic harmony, would be included in this category. Winge's other terms, "pathozygoty" and "misozygoty," refer to gametic relationships between hybrid parents in which syngamy is accomplished under very abnormal circumstances, or not at all.

This study has been carried on under the direction of Professor R. A. Harper and Professor J. S. Karling, whose continued encouragement and advice I gratefully acknowledge.

SUMMARY

1. Müller's report of pairing of chromosomes in root tip mitoses in three species of *Yucca* is here confirmed for *Yucca rupicola* Scheele.

2. Ten large and fifty small chromosomes are present in each diploid nucleus.

3. Chromosome pairing is likewise shown to be present in other embryonic zones, such as developing ovaries.

4. In the first division of the zygote nucleus and in later mitoses in developing embryos the chromosomes are arranged in pairs.

5. No definite arrangement of homologous chromosomes was observed in the endosperm nuclei.

6. If organisms are classified on the basis of the promptness with which their gametic complements come together after the beginning of the diploid state, *Yucca* is so far one extreme in such a series.

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Explanation of plates 11 and 12

In studying the preparations a Bausch and Lomb microscope was used. Figures were drawn with a camera lucida, using the 100× oil immersion objective and the 12.5× and 7.5× oculars. The magnification of all figures is 2300, except figures 9 and 12, which are magnified 1250 times.

Figs. 1, 2, and 3. Polar views of equatorial plate stages from root tip.

Fig. 4. Anaphase from a root tip cell.

Figs. 5 and 6. Polar views of equatorial plate stages from developing ovary.

Fig. 7. Polar view of an equatorial plate from an embryo of 500 to 1000 cells.

Fig. 8. Oblique view of an equatorial plate from an embryo of three or four cells.

Fig. 9. A three celled embryo, showing a telophase stage of mitosis in the terminal cell.

Fig. 10. A prophase stage from a cell of a young filamentous embryo.

Fig. 11. Reconstructed polar view of the equatorial plate stage shown in the median cell of the embryo shown in fig. 12.

Fig. 12. A five-celled embryo.

Fig. 13. An enlarged drawing of the median cell of the embryo in the preceding figure.

Fig. 14 (a and b). An embryo of one cell in a late prophase of the first embryonic mitosis. The cell was cut in the sectioning and hence appears in adjacent sections on the slide.

Fig. 15. The equatorial plate stage of the first embryonic mitosis.

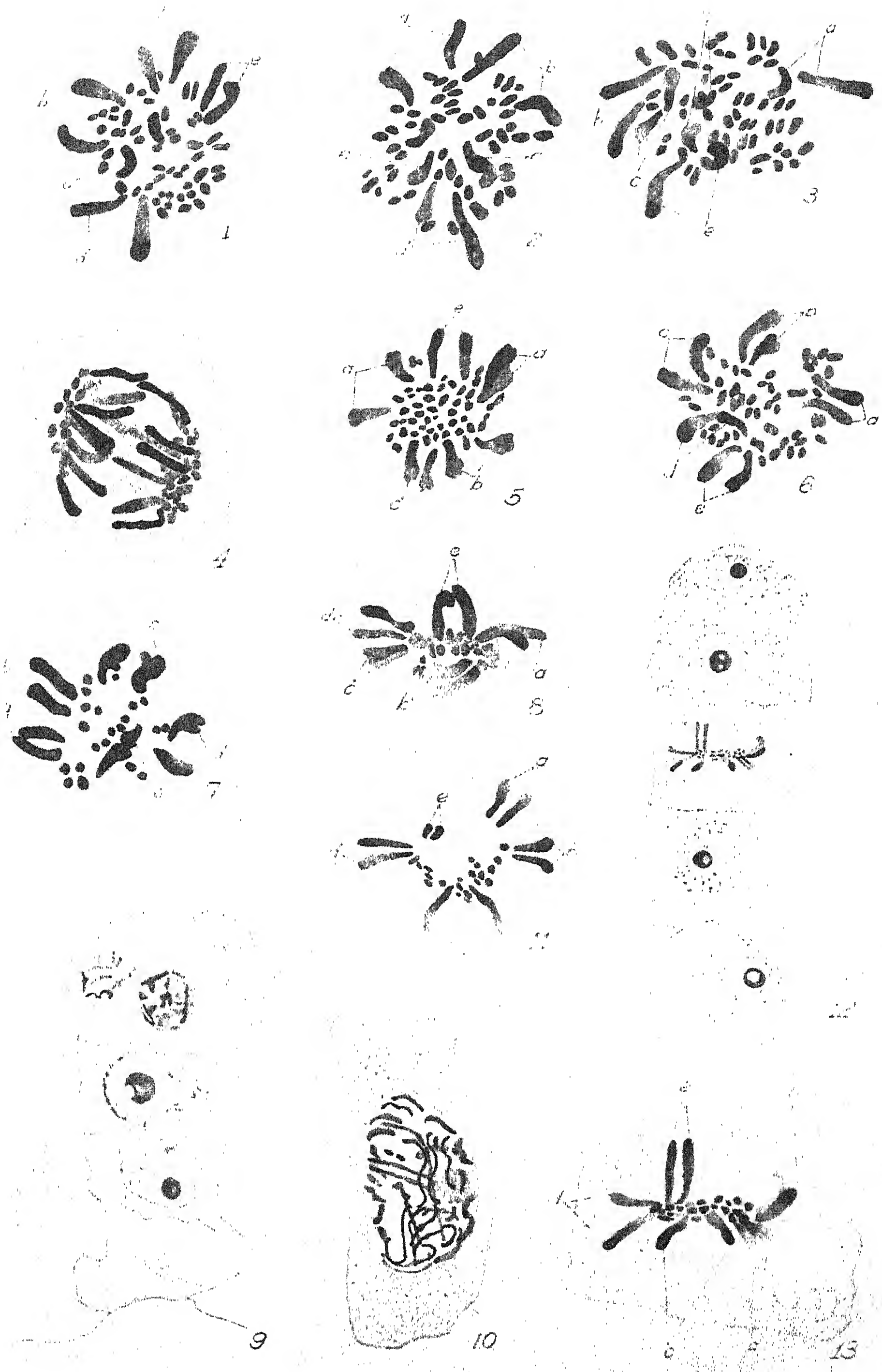
Fig. 16. Early anaphase of the first embryonic mitosis.

Fig. 17. Later anaphase of the first embryonic mitosis.

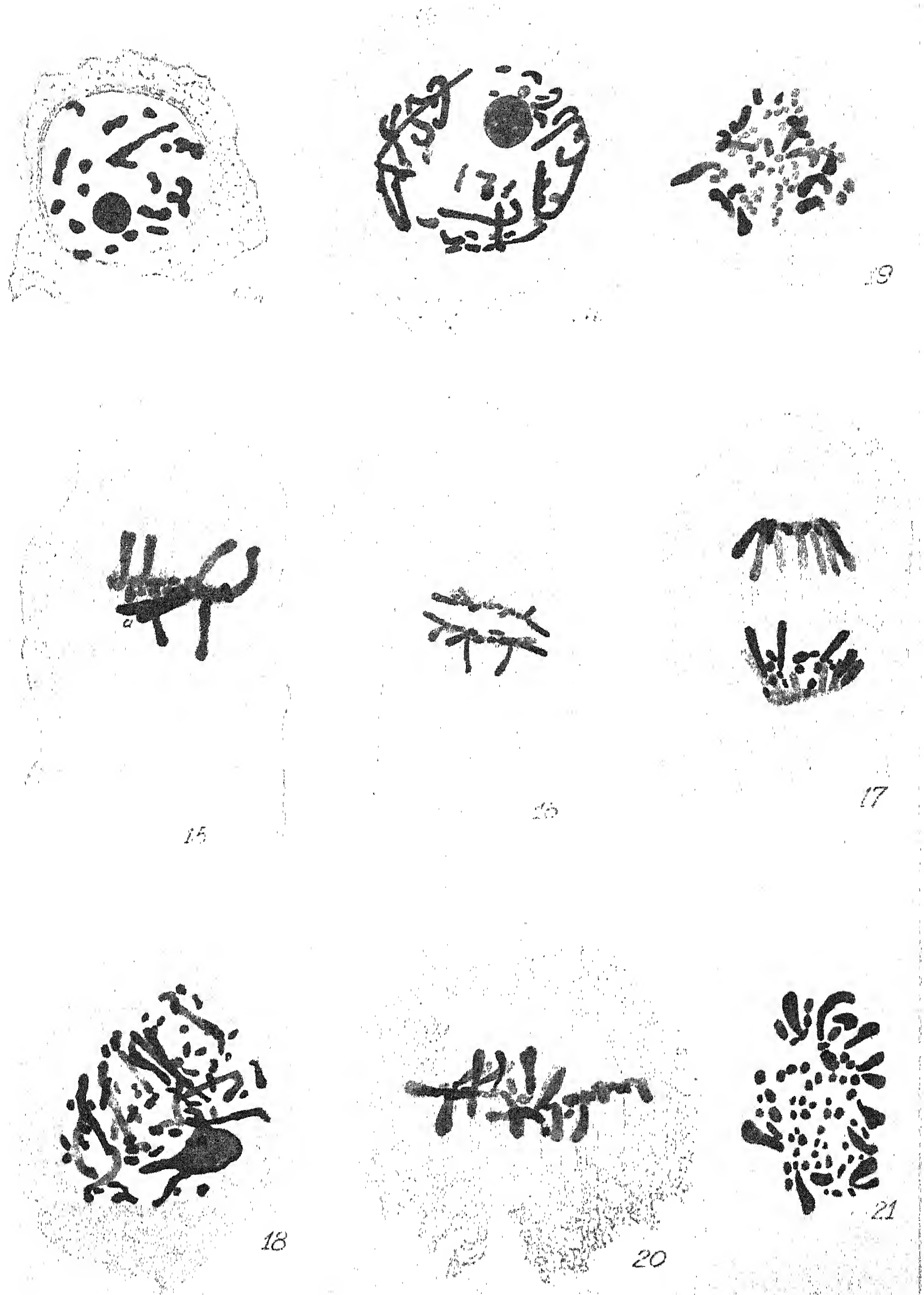
Fig. 18. Late prophase of free nuclear division in endosperm.

Fig. 19. Later prophase of endosperm mitosis after the nuclear membrane has disappeared.

Figs. 20 and 21. Equatorial plate figures in the endosperm.



WATKINS: YUCCA



WATKINS: YUCCA

Effects of ultra-violet radiation and temperature on Fusarium
II. Stimulation

ELIZABETH C. SMITH

(WITH FOUR FIGURES)

INTRODUCTION

The phenomenon of stimulation has been in dispute for some time. It has been considered by many as an irregular sort of process whose occurrence is unpredictable. Because of this irregularity the subject has aroused considerable interest, and for the same reason data concerning it are very meager in the literature. The data which will be presented in this paper indicate that at least in certain cases stimulation is predictable and its magnitude can be controlled by controlling certain environmental factors.

The lethal action of ultra-violet radiation and temperature on *Fusarium Eumartii* Carp. has already been discussed (Smith, 1935). The same species has been used in a study of the stimulation of vegetative growth and of spore production.

STIMULATION OF VEGETATIVE GROWTH

Methods

A suspension of spores was made in sterile distilled water. The spore load (the number of spores in 1 cc. of water) was determined with a Levy counting chamber. Enough of the suspension was added to sterile distilled water to give a spore load of not more than 40. One cubic centimeter was then plated out on a soft gelatin medium. The medium was prepared as follows: 200 grams of fresh potato slices were placed in 500 cc. of distilled water and the mixture was autoclaved at 15 pounds pressure for 20 minutes. One hundred grams of gelatin were dissolved in 500 cc. of warm distilled water. The two mixtures were combined, 30 grams of dextrose were added and the solution was diluted with distilled water to 1 liter. The pH was adjusted to 6.6 by the colorimetric method. The medium was sterilized in an Arnold steam sterilizer for 30 minutes on two successive days. About 72 hours after plating out the spores the colonies were large enough to transplant to agar. A scalpel dipped in alcohol and flamed was used to make the transfer. Single colonies were picked up with the tip of the scalpel and transferred in a sterile chamber to agar plates. Because of the softness of the gelatin medium only a small amount of gelatin adhered to the colonies. Three colonies were placed in each Petri dish. The agar used was a potato-dextrose agar. The preparation of this has already been described (Smith, 1935). For one experiment a so-called "poor" agar was

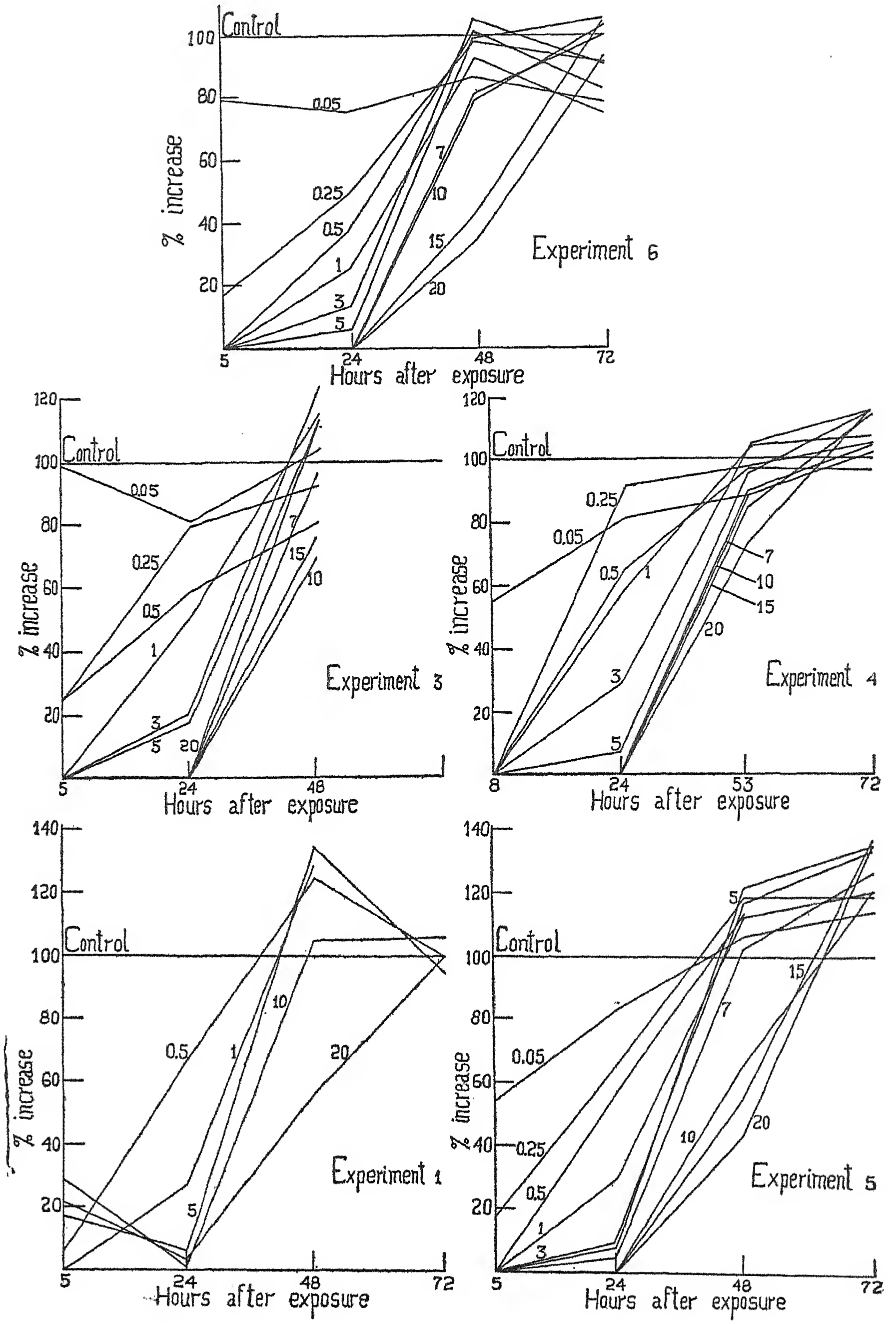


Fig. 1. Stimulation of vegetative growth as shown by the comparative growth rates of irradiated and control cultures during various intervals of time following irradiation. The period of irradiation in minutes is indicated on each curve.

TABLE 1

The mean increase in diameter (in mm. and as % of control) of irradiated and control cultures during various intervals of time following irradiation.

EXP. NO.	MINUTES EXPOSURE	0–5 HRS		5–24 HRS.		24–48 HRS.		48–72 HRS.	
		AV	%	AV.	%	AV.	%	AV.	%
1	Control	2.12	100.0	6.00	100.0	7.37	100.0	8.75	100.0
(12)*	0.5	0.12	5.6	4.12	68.6	9.25	125.5	8.75	100.0
	1	0.00	0.0	1.75	27.2	9.50	128.8		
	5	0.37	17.4	0.37	6.1	10.00	135.6	8.33	95.2
	10	0.62	29.2	0.12	2.0	7.75	105.3	9.25	105.7
	20	0.45	21.2	0.25	4.1	4.87	66.0	8.75	100.0
3	Control	1.34	100.0	5.52	100.0	7.17	100.0		
(33)	0.05	1.33	99.2	4.51	81.7	7.45	103.9		
	0.25	0.36	26.8	4.45	80.6	6.65	92.7		
	0.5	0.35	26.1	3.25	58.8	5.76	80.3		
	1	0.00	0.0	2.81	50.9	8.36	116.5		
	3	0.00	0.0	1.10	19.9	8.93	124.5		
	5	0.00	0.0	1.00	18.1	8.08	112.7		
	7	0.00	0.0	0.00	0.0	7.00	97.6		
	10	0.00	0.0	0.00	0.0	5.06	70.5		
	15	0.00	0.0	0.00	0.0	5.56	77.5		
	20	0.00	0.0	0.00	0.0	8.10	112.9		
4**	Control	1.75	100.0	4.07	100.0	8.11	100.0	5.22	100.0
(66)	0.05	0.97	55.4	3.32	81.5	7.24	89.2	5.35	102.5
	0.25	0.00	0.0	3.75	92.1	7.86	96.9	5.48	104.9
	0.5	0.00	0.0	2.67	65.6	7.85	96.8	5.07	97.1
	1	0.00	0.0	2.40	58.9	8.56	105.3	5.58	106.8
	3	0.00	0.0	1.16	28.5	8.45	104.2	6.22	119.1
	5	0.00	0.0	0.29	7.1	7.79	96.0	6.23	119.3
	7	0.00	0.0	0.00	0.0	7.30	90.0	5.44	104.2
	10	0.00	0.0	0.00	0.0	7.13	87.9	5.47	104.8
	15	0.00	0.0	0.00	0.0	7.33	90.3	6.06	116.0
	20	0.00	0.0	0.00	0.0	6.01	74.1	6.11	117.0
5	Control	1.46	100.0	5.75	100.0	6.83	100.0	5.52	100.0
(66)	0.05	0.79	54.1	4.85	84.3	7.31	107.0	6.35	115.0
	0.25	0.27	18.4	3.80	66.0	8.14	119.1	6.62	119.9
	0.5	0.00	0.0	3.30	57.3	7.80	114.2	6.35	115.0
	1	0.00	0.0	1.77	30.7	7.80	114.2	6.66	120.7
	3	0.00	0.0	0.42	7.3	8.35	122.2	7.50	135.9
	5	0.00	0.0	0.57	9.9	7.98	116.8	7.42	134.4
	7	0.00	0.0	0.32	5.5	6.99	102.3	7.02	127.1
	10	0.00	0.0	0.00	0.0	4.52	66.1	6.68	121.0
	15	0.00	0.0	0.00	0.0	3.83	56.0	7.61	137.8
	20	0.00	0.0	0.00	0.0	3.02	44.2	7.44	134.8
6	Control	1.15	100.0	5.91	100.0	7.62	100.0	7.54	100.0
(65)	0.05	0.90	78.2	4.50	76.0	6.61	86.7	5.87	77.8
	0.25	0.20	17.4	4.18	70.7	7.50	98.4	6.92	91.7
	0.5	0.00	0.0	3.42	57.8	7.68	100.8	6.28	83.3
	1	0.00	0.0	1.53	25.8	7.13	93.5	5.60	74.2
	3	0.00	0.0	0.85	14.3	7.99	104.8	6.91	91.6
	5	0.00	0.0	0.36	6.0	7.51	98.5	8.00	106.1
	7	0.00	0.0	0.00	0.0	6.22	81.6	7.55	100.1
	10	0.00	0.0	0.00	0.0	6.13	80.4	7.74	102.6
	15	0.00	0.0	0.00	0.0	4 81	63.1	7.94	105.3
	20	0.00	0.0	0.00	0.0	4.17	54.7	7.00	92.8

* Numbers in parentheses indicate number of colonies used.

used. This was made with lactose and Duggar's modification of Richard's solution. Twenty-five cc. of M/2 lactose, 10 cc. of M/1 KNO_3, 10 cc. of M/4 KH_2PO_4, 5 cc. of M/10 $MgSO_4$ and a trace of iron were substituted for the potato and dextrose in the usual potato-dextrose agar. Otherwise the medium was prepared as before.

All cultures were allowed to grow for 24 hours before irradiation with ultra-violet. In some experiments the cultures were placed in an incubator at 30°C., in some they were grown at the temperature of the laboratory (about 25°C.) and in other experiments they were grown at 21°C. During this period the cultures became adjusted to the agar medium and a normal growth rate was established.

Just before irradiation the colonies were measured. Two lines were drawn at approximately right angles to each other on the bottom of the Petri dish, intersecting at the center of each colony. Measurements were made with the aid of a binocular dissecting microscope set on a ground glass plate illuminated from below. A piece of millimeter graph paper was placed on the plate to serve as a scale. The covers were removed from the dishes to facilitate measuring. By focusing the microscope on the graph paper and the colony, measurements could be made which were accurate to within 1 to 2 tenths of a millimeter. The widths of each colony were measured along the two lines.

A Cooper-Hewitt mercury arc lamp operating at 7.5 amperes and 110 volts served as a source of ultra-violet radiation. The lamp was allowed to run for at least 30 minutes before each experiment so that the intensity of the radiation was fairly constant. The full spectrum of the lamp was employed. In this paper unless it is otherwise stated reference to ultra-violet so far as it is used experimentally includes some infra-red and some visible radiation. This liberty is taken with the assumption that biological effects are due, as the extensive literature seems to indicate, to energy in the ultra-violet exclusively or practically so.

The uncovered cultures were given different exposures to radiation in a constant temperature bath at 0°C. The distance between the lamp and the culture was 40 cm. except in one set of experiments in which this distance was increased to 150 cm. After irradiation the cultures were allowed to grow either at the temperature of the laboratory (about 25°C.), at 30°C. or at 21°C. At intervals the colonies were measured along the same lines as before.

The principal sources of error in this method are the limitations on the number of individuals which can be measured in a single experiment and the presence of by-products in the medium which affect the growth rate of older cultures.

Data and results

Table 1 gives the comparative rates of growth of irradiated and control cultures during various intervals of time following irradiation. The same results are represented graphically in figure 1. For these data the colonies were grown at the temperature of the laboratory (about 25°C.) before and after irradiation. Stimulation of the growth rate did not occur except after a previous retardation of growth, and the amount of stimulation in any one experiment is roughly proportional within certain limits to the amount of previous retardation. This is shown by the growth averages in table 1. This

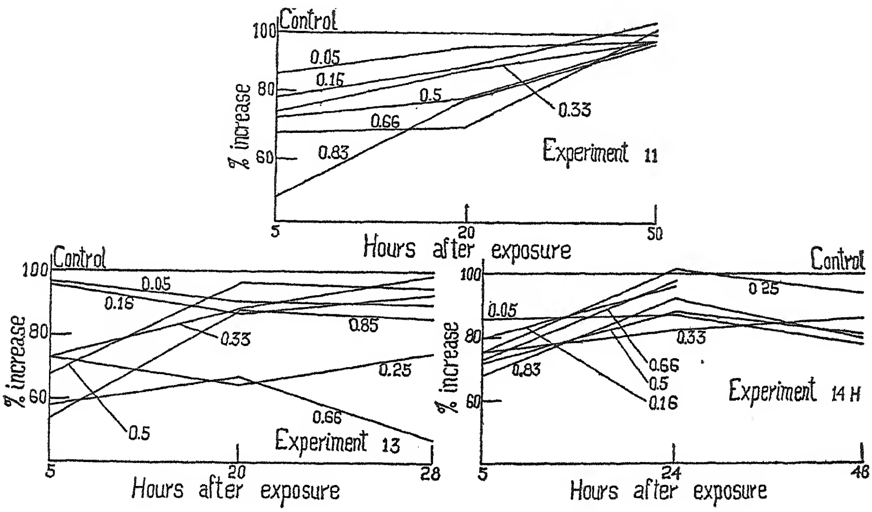


Fig. 2. The lack of initial stimulation with short exposures to radiation as shown by the comparative growth rates of irradiated and control cultures during various intervals of time following irradiation. The period of irradiation in minutes is indicated on each curve. The cultures were irradiated at 150 cm. instead of at 40 cm. as in the other figures.

table also shows that with every exposure to radiation the total increase in diameter is less than in the controls. In general the maximum amount of stimulation occurs during the 24–48 hour interval after exposures of 3 or 5 minutes. The initial retardation bears a direct relation to the length of the exposure. The growth obtained with 15 and 20 minute exposures is quite variable so that averages for these long exposures are not so significant. After 72 hours growth becomes quite variable owing perhaps to the accumulation of harmful by-products in the medium. Also the averages obtained for 72 hours are usually based on a smaller number of measurements. By this time the colonies had frequently become so crowded that accurate measurements could not be made.

The fact has been emphasized that stimulation of the growth rate does not occur except after a previous retardation. Frequent reports in the literature of an initial stimulation with small doses of ultra-violet radiation led to the experiments recorded graphically in figure 2. For these experiments the distance between the lamp and the culture was increased from 40 to 150 cm. The amount of energy from a 40-second exposure at 150 cm. is roughly equivalent to that from a 3-second exposure at 40 cm., and that from a 3-second exposure at 150 cm. is roughly equivalent to that from 3/14 of a second at 40 cm. In no case was there any initial stimulation.

Many cases have been reported of a stimulation of the growth rate with ultra-violet radiation and with X-rays. Most of the early workers regarded stimulation as a direct result of irradiation. The tendency in recent years, however, has been to regard stimulation as a result of a previous retardation resulting from the action of the rays. It is rather generally believed that the earlier workers fell into error because of the small number of individuals used in their experiments. Hutchinson and Ashton (1930) reported growth stimulation following retardation when *Colletotrichum phomoides* is exposed to ultra-violet. Many workers have reported growth stimulation following retardation after treatment with X-rays. If stimulation is a direct result of a previous checking of the growth rate and not a direct result of irradiation, then it should follow that when the growth rate is checked temporarily by any kind of agent, stimulation should result when growth is resumed. This seems frequently to occur. Miss Colley (1931) reported that cells of *Escherichia coli* are initially inhibited when grown in 0.0001 N and 0.00025 N $ZnSO_4$, but after 16 to 20 hours they increased in number so that after 24 hours the colonies were 9 per cent larger than the controls. In other bacteria, however, she observed an initial stimulation. Townsend (1897) reported retardation and a subsequent stimulation of growth of barley and corn seedlings following mechanical injuries. However, he reported also an initial acceleration with very slight injuries. Experiments were made by the author with low temperatures on *Fusarium Eumartii*. An exposure of 5 hours to 0°C. or 45 minutes to −7.5°C. produced a marked retardation followed by stimulation. Shorter exposures or higher temperatures, or both, never produced an initial stimulation. These results are in agreement with those obtained with ultra-violet radiation. They support the idea that stimulation is not due to something inherent in radiation alone but to something characteristic of a number of factors whose only common property is their ability to inhibit growth. This does not preclude the possibility of an initial stimu-

lation. Its existence, however, will be questioned until there has been adequate verification with quantitative methods.

The amount of stimulation recorded in table 1 varies markedly in different experiments. It was considered that certain environmental conditions might affect the amount of stimulation produced. This question was discussed by Hutchinson and Newton (1930) for yeasts. In their experiments with visible light they always obtained the greatest stimulation when the control had a slow rate of growth. On the other hand, Shull and Mitchell (1933) using X-rays reported that harmful effects mask stimulation of the growth rates of wheat, corn, oats and sunflower. They considered brief exposures, the use of metallic screens, high voltage, and low amperage as favorable conditions for producing stimulation with X-rays. I have made attempts to determine the effects of two environmental factors, temperature and the quality of the medium, on stimulation following irradiation. To determine the possible effects of temperature on stimulation cultures were irradiated at 0°C. at 40 cm. from the lamp and grown either at 30°C. or at 21°C. In general stimulation was greater in cultures grown at the higher temperature. The experiments were, however, not carried out for a long enough period of time to show that stimulation was not merely delayed by the lower temperature. Experiments extending over a longer period of time and with a wider temperature range are necessary before definite conclusions can be drawn. The experiments seem to indicate, however, that temperatures favorable for a rapid growth rate may also be favorable for stimulation. When an agar is used which does not favor growth there is less stimulation. This is shown in table 2 and figure 3. In experiment 2 a potato-dextrose agar was used which was accidentally partly precipitated. Spores would not germinate on this agar and mycelial growth was very slow. A so-called "poor" agar in which lactose was the source of carbon was used in experiment 10P. The preparation of this agar has already been described. In 10G the usual potato-dextrose agar was used. The cultures were grown at 30°C. in experiments 10G and 10P and at about 25°C. in experiment 2. If results could be obtained for other environmental factors similar to those obtained for temperature and the quality of the medium, then it could be stated that any factor favorable to the growth of the culture is favorable also to stimulation. The results reported here at least suggest this conclusion.

Previous workers have suggested that when growth is retarded labile products may be stored in the plant until conditions are again favorable for growth. It seems possible that growth acceleration results immediately following retardation because of this accumulated supply of labile products. If this is the case it does not seem unreasonable to assume that any

TABLE 2

The mean increase in diameter (in mm. and as % of control) of irradiated and control cultures during various intervals of time following irradiation. Experiments 2 and 10P were made with poor nutrient agars and experiment 10G with a good nutrient agar.

EXP. NO.	MINUTES EXPOSURE	0–24 HRS.		24–48 HRS.		48–72 HRS.	
		AV.	%	AV	%	AV.	%
10G	Control	9.04	100.0	8.78	100.0	8.32	100.0
(45)*	0.05	7.98	88.2	9.22	105.0	9.10	109.3
	0.25	6.79	75.1	9.03	102.8	8.85	106.3
	0.5	5.20	57.5	9.30	105.9	8.77	105.4
	1	4.58	50.6	9.80	111.6	9.47	113.8
	3	2.40	26.5	9.85	112.1	9.33	112.1
	5	2.68	29.6	10.23	116.4	8.93	107.3
	7	0.60	6.6	9.80	111.6	8.16	98.0
	10	0.54	5.9	9.17	104.4	9.20	110.6
	15	0.00	0.0	9.31	106.0	8.85	106.3
10P	Control	7.49	100.0	7.77	100.0	6.91	100.0
(55)	0.05	6.43	85.8	8.23	105.9	7.95	115.0
	0.25	4.59	61.2	7.42	95.5	8.43	121.9
	0.5	2.91	38.8	7.74	99.6	8.24	119.2
	1	0.41	5.4	9.63	123.9	7.93	114.7
	3	0.00	0.0	3.75	48.2	8.68	125.6
	5	0.00	0.0	3.65	46.9	9.32	134.8
	7	0.00	0.0	2.30	29.6	8.33	120.5
	10	0.00	0.0	1.65	21.2	8.70	125.9
	15	0.00	0.0	0.00	0.0	5.60	81.0
2**	Control	0.60	100.0	5.60	100.0	4.30	100.0
(33)	0.05	0.75	125.0	4.46	79.6	4.11	95.5
	0.25	0.17	28.3	3.75	66.9	3.60	83.7
	0.5	0.10	16.6	3.75	66.6	4.23	98.3
	1	0.07	11.6	3.32	59.2	4.17	96.9
	3	0.07	11.6	1.95	34.8	3.85	89.5
	5	0.06	10.0	1.61	28.7	3.65	84.8
	7	0.06	10.0	1.08	19.2	3.28	76.2
	10	0.10	16.6	2.10	37.5	3.81	88.6
	15	0.05	8.3	0.85	15.1	3.22	74.8
	20	0.01	1.6	0.52	9.2	2.52	58.6

* Numbers in parentheses indicate number of colonies used.

** Colonies measured after 5, 31 and 48 hours.

factor which favors the formation of labile products also favors stimulation following retardation. One might also expect that any factor which would increase the growth rate of controls would increase the formation of labile products in exposed cultures. This theory involving labile products is purely hypothetical but it does offer a rather satisfying explanation of the results obtained here and in the investigations reported by others. It does not, however, give any explanation for cases reported of initial

stimulation. The possibility certainly exists that experiments which show initial stimulation were so designed that a retardation might have occurred unobserved. It is difficult, for example, to conceive of a mechanical

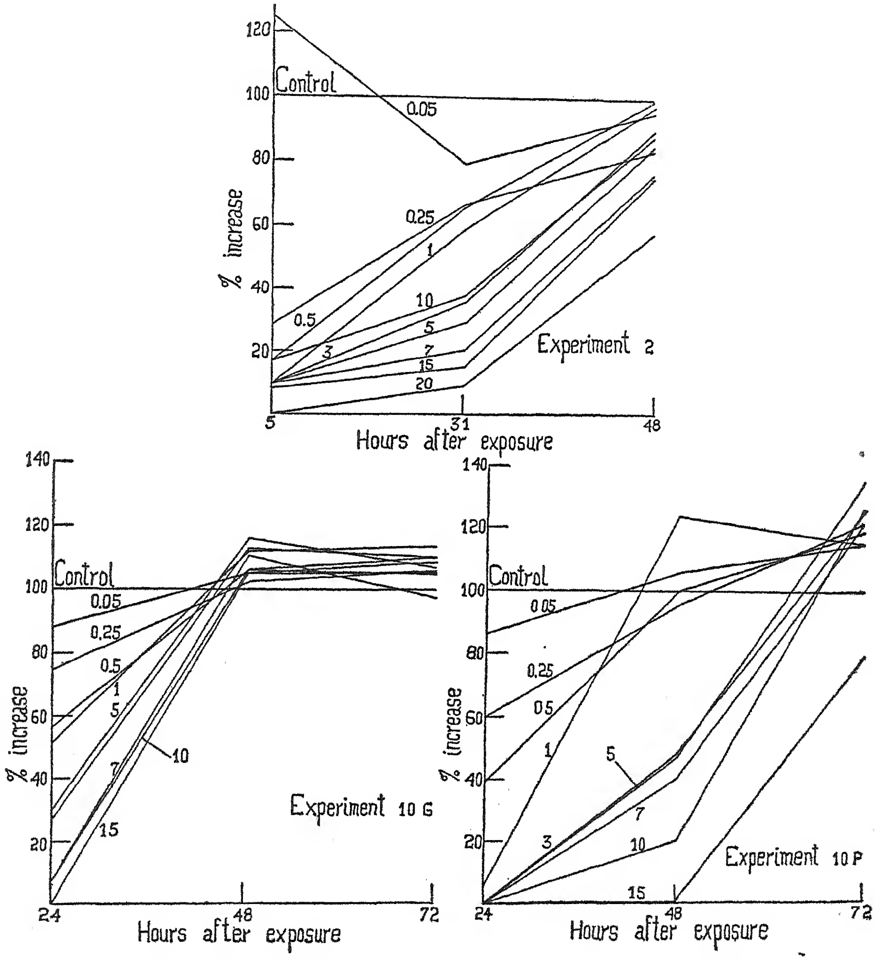


Fig. 3. The depressing effect on stimulation of a poor nutrient medium as shown by comparative growth rates of irradiated and control cultures during various intervals of time following irradiation. The period of irradiation in minutes is indicated on each curve. Experiments 2 and 10P were made with poor nutrient agars and experiment 10G with a good nutrient agar.

injury to a seedling which does not at least temporarily interrupt growth in some part. The mass of the literature demands an hypothesis involving growth retardation.

STIMULATION OF SPORE PRODUCTION

Methods

Some of the cultures used for growth-rate measurements were used also for measurements of spore production. Only cultures were used which were irradiated at 40 cm. from the lamp. To measure spore production a disc 18.5 mm. in diameter was cut with a sharpened cork borer from the center of each culture 72 hours after irradiation. Since the colonies were approximately this diameter when irradiated the results are based on spores produced on irradiated mycelium and not on mycelium produced following irradiation. Each disc was placed in 25 cc. of water in a flask. Since some time was required to make spore counts a 5 per cent aqueous

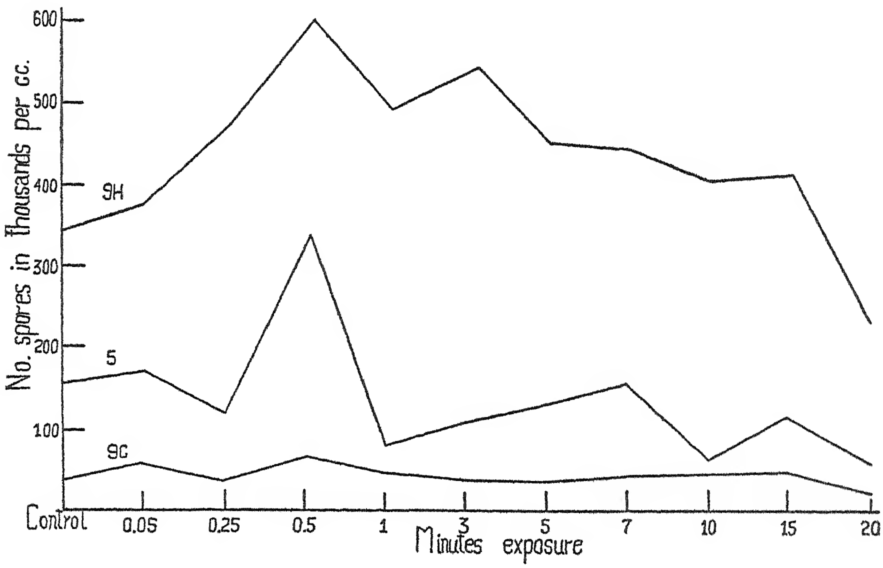


Fig. 4. Stimulation of spore production as shown by the relative numbers of spores produced in control and irradiated cultures grown at 30°C. in experiment 9H, at about 25°C. in experiment 5 and at 21°C. in experiment 9C.

solution of formalin instead of distilled water was sometimes used to prevent spore germination. The number of spores per cubic centimeter of spore suspension was determined with a Levy counting chamber. It is very important that the suspension be thoroughly shaken to dislodge all the spores from the mycelium before counts are made. To insure this the suspension was thoroughly shaken before each sample was taken. In each case samples were drawn until there was fairly close agreement between consecutive counts.

Data and results

Table 3 and figure 4 show the number of spores per cubic centimeter of suspension produced in cultures exposed to various amounts of ultra-violet radiation. The maximum amount of spore production occurred in each experiment with a 30-second exposure regardless of the temperature at which the cultures were grown and consequently of the rate of growth of the culture. The number of spores produced was very much greater when the cultures were grown at 30°C. than when grown at 21°C. With an intermediate temperature such as that of the laboratory (about 25°C.) the number of spores produced was also intermediate. There were about eight times as many spores in the controls grown at 30°C. as in those grown at 21°C. and about twice as many as at 25°C. This shows that temperature alone is effective in increasing spore production. The effects of temperature and ultra-violet are not additive when the two are present together since the three curves in figure 4 do not all show the same amount of stimulation above the controls. The effects of temperature differ here, as for lethal action, depending on whether the temperature acts alone or in conjunction with ultra-violet radiation.

Stevens (1930), Hutchinson and Ashton (1930), Ramsey and Bailey (1930), Porter and Bockstahler (1928) and others have reported a stimulation of spore production by ultra-violet radiation. Many of these workers, however, have either disregarded the effects of temperature or have considered them unimportant. Ramsey and Bailey reported that temperature is not an important factor in determining sporulation in *Macrosporium tomato* and *Fusarium Cepae*. They considered the effects of ultra-violet and of temperature in separate experiments and did not consider the effect of temperature in conjunction with ultra-violet radiation. Stevens regarded the rise in temperature of a culture during irradiation as unimportant with regard to its effects on spore production. The author finds, however, that the number of spores produced by *Fusarium Eumartii* can be so increased with a 2-minute exposure to ultra-violet in the absence of a temperature control that the whole culture becomes distinctly blue in color. The blue color is due to diffraction by a large number of spores and not to pigmentation. The blue color was not obtained when the cultures were irradiated in ice water or in a water bath at room temperature. With this fungus, at least, an accurate measure of spore production under the influence of ultra-violet radiation cannot be obtained without temperature control.

It is rather generally considered that spores are produced only when there is a retardation of vegetative growth. This raises the question as to

TABLE 3

The effects of ultra-violet on spore production in cultures grown at different temperatures.

EXP. NO.	TEMPERATURE °C.	MINUTES EXPOSURE	AV. NO. SPORES/CC. OF SUSPENSION
5	25	Control	156,700
(39)*		0.05	171,000
		0.25	120,000
		0.5	336,000
		1	78,500
		3	112,700
		5	128,500
		7	155,000
		10	68,700
		15	116,500
		20	59,200
9H	30	Control	336,200
(56)		0.05	374,100
		0.25	476,100
		0.5	602,100
		1	484,000
		3	542,000
		5	452,600
		7	442,700
		10	397,000
		15	405,000
		20	230,300
9C	21	Control	39,700
(61)		0.05	61,800
		0.25	40,400
		0.5	62,500
		1	50,800
		3	44,600
		5	45,800
		7	44,500
		10	48,000
		15	57,500
		20	22,800

* Numbers in parentheses indicate number of colonies used.

whether the stimulation of spore production with ultra-violet radiation arises from a retardation of the growth rate following irradiation. A study of growth rates with a 30-second exposure, however, reveals nothing which might explain a maximum spore production with this exposure. Also many factors which affect the growth rate apparently do not influence spore production. These facts do not prove but they do indicate that it is very likely that ultra-violet acts directly here as a stimulant to spore produc-

tion. If this is so, the manner of stimulation of spore production forms an interesting contrast to that of stimulation of the growth rate.

SUMMARY

1. Stimulation of vegetative growth was never obtained without a previous retardation, and even when stimulation occurred the total growth was never greater than in the controls. There were no cases of an initial stimulation. Stimulation is considered as merely an indirect effect of radiation and a direct effect of retardation since other agents which produce a retardation also produce stimulation. Temperature conditions and nutritional conditions which favor the growth of the fungus favor also stimulation. The idea is suggested that those conditions which favor the formation and accumulation of labile products favor also stimulation following retardation.

2. The maximum stimulation to spore production occurs with a 30-second exposure to ultra-violet radiation regardless of the growth rate of the fungus. Temperature alone is effective in stimulating spore production. Since the amount of stimulation with ultra-violet is different in cultures grown at different temperatures the effects of ultra-violet and temperature are not additive. Since a study of growth rates reveals nothing which might explain a maximum spore production with a 30-second exposure to ultra-violet and since many other factors which influence the growth rate have not been found to influence spore production, ultra-violet may act directly rather than indirectly to stimulate spore production.

This investigation was proposed by Prof. B. M. Duggar and has been carried on with his suggestions and criticisms. The author is indebted to Prof. Duggar and to Prof. H. H. Bartlett for assistance in the preparation of the manuscript. The latter part of this investigation was carried on at the University of Michigan with the aid of an F. C. and Susan Eastman Newcombe Fellowship.

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INDEX TO AMERICAN BOTANICAL LITERATURE

1931–1934

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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Inheritance of resistance to loose smut in hybrids of Fulghum and Black Mesdag oats[1]

George M. Reed

The present paper is concerned with the results obtained in an investigation of the inheritance of resistance to the Fulghum race of loose smut of oats in hybrids between Fulghum and Black Mesdag. The investigations of Reed (1927, 1929), and Reed and Stanton (1932) have demonstrated the existence of specialized races of both loose (*Ustilago Avenae* (Pers.) Jens.) and covered (*U. levis* (K. & S.) Magn.) smuts of oats which severely attack the Fulghum group of red oats. Several collections of these smuts have been obtained on Fulghum from various sources. Some other oat varieties, such as Canadian and Victor, have also proved to be susceptible. Fulghum, however, is very resistant to other highly specialized races of both oat smuts.

Black Mesdag has shown a high degree of resistance to all known races of loose smut, including the Fulghum race. No plants inoculated with the loose smut collected on Fulghum have been infected. It may be noted, however, that Black Mesdag has been found to be susceptible to a race of covered smut which is characterized by its ability to infect the Fulghum group of red oats (Reed 1932b).

Four crosses between Fulghum and Black Mesdag (Hybrids 29 to 32) were made in 1926, Fulghum being used as the female parent, and the first generation plants were grown in 1927. In 1928, inoculated F_2 plants were grown, some in the greenhouse and others in the field. Additional inoculated plants were grown in the field in 1929, and some uninoculated plants in 1931. Third, fourth, and fifth generation progenies were grown in various seasons from 1929 to 1934.

In all the experiments in which these hybrids were inoculated with loose smut, collection No. 13 was used. This collection was made by Mr. T. R. Stanton, Office of Cereal Crops and Diseases, Bureau of Plant Industry, Washington, D. C., on Fulghum oats at Lawton, Okla., in June 1925, and it was one of the original collections upon which the differentiation of the Fulghum race of loose smut was based.

The methods employed were those which have been used in all of my studies on the inheritance of smut resistance. The hulls were removed from the caryopses, which were then inoculated by dusting with the dry spores and germinated at a temperature of approximately 20°C. in sand

[1] Brooklyn Botanic Garden Contributions No. 70.

[The Bulletin for March (62: 117–176) was issued March 1, 1935]

with a low moisture content. Under these conditions, the seedlings usually emerged in four days and two to three days later were transplanted.

EXPERIMENTAL RESULTS WITH THE F_2 GENERATION

In table 1 are recorded the results obtained with the inoculated second generation plants of the four hybrids and also the two parental varieties. The data for the latter include all the results secured during 1928 to 1934, when they were grown along with the F_2 and later hybrid generations.

TABLE 1

Data obtained with the F_2 generation of hybrids 29–32—Fulghum×Black Mesdag, inoculated with Ustilago Avenae—Fulghum.

HYBRID NO.	NO. PLANTS	NO. INFECTED	PER CENT INFECTED
29	133	21	15.7
30	132	24	18.1
31	128	27	21.0
32	107	18	16.8
	500	90	18.0
		Reaction of parental varieties	
Fulghum	246	181	73.5
Black Mesdag	224	0	0

From the table, it will be noted that Fulghum gave 73.5 per cent infection, 181 plants out of a total of 246 being infected. In very few experiments were all of the Fulghum plants smutted. In contrast to Fulghum, Black Mesdag gave completely negative results; altogether, 224 plants were grown and none was infected.

In 1928 and 1929, 500 second generation plants belonging to the four hybrids were inoculated, and 90 (18 per cent) were infected. The percentage of infection in the four hybrids varied from 15.7 in Hybrid 29, to 21 per cent in Hybrid 31. The results indicate that resistance to smut is dominant and that segregation in the F_2 generation may occur on the basis of a three to one ratio.

EXPERIMENTAL RESULTS WITH THE F_3 GENERATION

There were two distinct groups of F_3 progenies available for study. (1) A group descended from F_2 plants which had been inoculated and survived, and (2) a group descended from F_2 plants which had not been inoculated. Results obtained with both groups of F_3 progenies are summarized in the distribution table 2. In this table the progenies are separated into classes,

based upon the percentage of infection. The number of progenies in each class, together with the total number of plants, the number infected, and the per cent infected, are shown. The reactions of the two groups of F_3 progenies are represented in the accompanying figure

TABLE 2

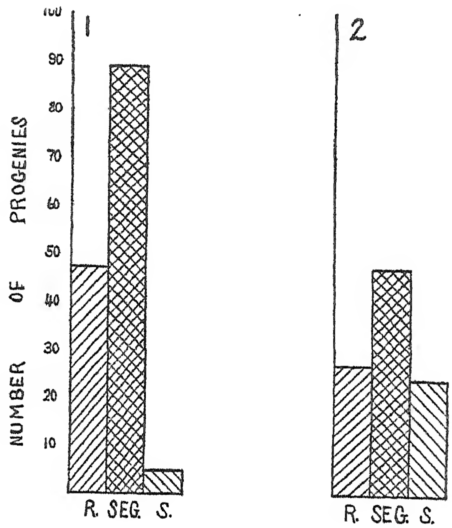
Data obtained with the F_3 generation of hybrids 29–32—Fulghum×Black Mesdag, inoculated with Ustilago Avenae—Fulghum.

CLASS CENTER	F_2 PLANTS INOCULATED WITH USTILAGO AVENAE—FULGHUM				F_2 PLANTS UNINOCULATED			
	NO. OF PROGENIES	NO. OF PLANTS	NO. INF.	PER CENT INF.	NO. OF PROGENIES	NO. OF PLANTS	NO. INF.	PER CENT INF.
0	47	1363	0	0	27	587	0	0
5	17	516	33	6.3	20	436	29	6.6
15	49	1293	190	14.6	12	257	38	14.7
25	17	495	123	24.8	5	110	27	24.5
35	3	78	30	38.4	4	92	29	31.5
45	3	67	32	47.7	6	139	65	46.7
55	2	62	34	54.8	5	114	63	55.2
65	0	0	0	0	6	128	83	64.8
75	1	24	18	75.0	6	130	99	76.1
85	1	20	17	85.0	4	97	83	85.5
95	1	24	23	95.8	3	67	62	92.5

On the basis of their reaction, the third generation progenies may also be classified as (1) resistant, in which no infected plants are found, (2) segregating, progenies in which the percentage of infected individuals is less than 50 per cent, and (3) susceptible, progenies which contain more than 50 per cent of smutted plants. The separation of the segregating and susceptible progenies is more or less arbitrary. It is possible that a segregating family consisting of 25 plants or less may contain more than 50 per cent of smutted individuals. A susceptible progeny also may show less than half of the plants infected. In general, however, the families may be distinguished on the basis indicated.

1. *F_3 progenies descended from inoculated F_2 plants.* As recorded in table 1, there were 500 F_2 plants inoculated, and 410 of these survived. Descendants of 141 of these plants were grown in the F_3 generation, the data being recorded in table 2. Of these, 47 progenies, containing 1363 plants, gave no infection, and are classified as resistant. There were 89 progenies classified as segregating, since they all contained some smutted plants, but the percentage of infection was less than 50 per cent. The 5

remaining progenies were classified as susceptible; 2 of these, however, were in the group whose class center is 55 per cent. Hybrid 31–F_3–93 grown in the field in 1929, contained 22 plants, of which 13 (59 per cent) were infected, and Hybrid 32–F_3–55 grown in the greenhouse in 1929, contained 40 plants of which 21 (52.5 per cent) were infected. These 40 plants were grown in two separate pots, and in one pot 10 plants were infected and in the other 11. The other 3 susceptible families gave 75, 85, and 95.8 per cent infection.



Reaction of F_3 progenies of Hybrids 29 to 32—Fulghum × Black Mesdag—to *Ustilago Avenae*—Fulghum.

1. F_2 plants inoculated 2. F_2 plants not inoculated

R.—Resistant progenies—No plants infected

Seg.—Segregating progenies—Percentage of infection 50 per cent or less

S.—Susceptible progenies—More than 50 per cent of the plants infected

As already noted, the F_2 data indicate that segregation takes place on the basis of a ratio of three resistant to one susceptible. The percentage of susceptible F_2 plants was somewhat low—actually, one F_2 plant out of five was smutted. The result of inoculating the F_2 plants is the elimination of all or practically all of the susceptible individuals; hence they would not be available for growing F_3 progenies. Consequently, in this particular group of F_3 progenies, descended from inoculated plants, we might expect one resistant progeny to two segregating. The results obtained are fairly close to expectation, since 47 progenies were resistant and 89 segregating.

The 5 susceptible progenies recorded may be due to the fact that susceptible F_2 individuals escaped infection and thus survived for growing the following generation. There may be some question as to whether the two progenies giving between 50 and 60 per cent infected plants were susceptible or segregating. There can, however, be no reasonable doubt about the other three, which gave 75 per cent or more infection.

2. *F_3 progenies descended from uninoculated F_2 plants.* As recorded in table 2, there were 98 F_3 progenies grown from uninoculated F_2 plants. These were classified as 27 resistant, 47 segregating, and 24 susceptible. The 27 resistant progenies contained 587 plants. Of the 47 segregating progenies, 20 are found in the group whose class center is 5, 12 additional ones are found in the group whose class center is 15, and the remaining ones are distributed somewhat uniformly in the three groups with class centers of 25, 35, and 45.

The susceptible families are distributed in all the groups with class centers from 55 to 95. None of the progenies gave 100 per cent infection, but it may be noted again that the susceptible Fulghum parent rarely ever contained 100 per cent infected plants in a given experiment.

Since the F_2 plants had not been inoculated, the susceptible individuals were not eliminated; consequently, F_3 progenies might be grown from such susceptible plants. Further, if segregation in the F_2 generation takes place on the basis of a ratio of three to one, we would expect, among the F_3 progenies descended from uninoculated F_2 plants, 1 resistant, 2 segregating, and 1 susceptible. The results obtained harmonize fairly well with expectations.

EXPERIMENTAL RESULTS WITH THE F_4 GENERATION

A series of 256 F_4 progenies was grown in the course of the experiments. All of these had descended from uninoculated second generation plants. Most of them also had descended from uninoculated individuals of F_3 progenies. The reaction of the third generation, however, was known by the behavior of inoculated sister plants. The F_4 progenies were descended from three distinct types of F_3 families—resistant, susceptible, and segregating.

1. *F_4 families descended from resistant F_3 progenies.* There were 15 resistant F_3 progenies, represented by 3 to 11 F_4 families, a total of 108 being grown. These contained 1726 plants. Only 6 smutted plants, distributed among 5 different families, were observed. Thus the resistance manifested in the third generation is evident in the F_4 descendants.

2. *F_4 families descended from susceptible F_3 progenies.* There were 72 F_4 families grown from 16 F_3 progenies classified as susceptible, the percent-

ages of infection ranging from 54.1 to 95.4 per cent. All of the 72 F_4 families contained some smutted plants, although the amount of infection varied greatly, most of them giving more than 50 per cent infection. The lowest percentage was 7.1, while in two families all the plants were smutted.

Since the F_3 progenies were classified as susceptible, we might expect that all of the F_4 families would also be susceptible. However, many families contained entirely too few infected plants to be classified as susceptible. It is interesting to note the details for the F_3 progenies from which 5 or more F_4 families were grown.

F_3 generation—per cent inf.		*F_4 generation—per cent inf.*	
Hybrid 29–F_3–204	84.0	7 families	47.3– 78.9
" 29–F_3–210	80.0	5 "	58.8– 85.0
" 30–F_3–208	91.6	5 "	57.8– 89.4
" 31–F_3–207	90.4	5 "	10.5– 55.5
" 32–F_3–201	95.4	5 "	17.6–100.0
" 30–F_3–201	54.1	10 "	25.0– 75.0
" 31–F_3–210	70.0	5 "	50.0–100.0
" 32–F_3–205	68.1	10 "	7.1– 90.0

The first five F_3 progenies gave 80 to 95.4 per cent infection; among the F_4 families, however, the percentages ranged from 10.5 to 100 per cent. The last three F_3 progenies gave 54.1 to 70 per cent, and the range of infection in the F_4 generation varied from 7.1 to 100 per cent.

3. *F_4 families descended from segregating F_3 progenies.* There were 8 F_3 segregating progenies, represented by 76 F_4 families, the data for which may be summarized as follows:

F_3 generation—per cent inf.		*F_4 generation—range of infection*		
Hybrid 29–F_3–203	12.5	8 families		All resistant
" 29–F_3–205	8.3	8 "	resistant;	2 gave 5.0–10.5
" 30–F_3–202	4.0	6 "	"	4 " 6.2–12.5
" 30–F_3–204	5.0	10 "		All resistant
" 31–F_3–201	12.5	4 "	resistant;	6 gave 5.2–90.9
" 31–F_3–204	6.2	2 "	"	8 " 10.0–80.0
" 31–F_3–208	33.3	5 "	"	5 " 5.5–15.0
" 32–F_3–211	5.0	7 "	"	1 " 10.0

The results are not sufficiently extensive to furnish the basis for any definite conclusions. The behavior of some of the individual families, however, is particularly interesting. Hybrid 29–F_3–203 and Hybrid 30–F_3–204 contained some smutted plants, but all the F_4 families were completely resistant. Hybrid 32–F_3–211 contained 1 smutted plant, while in the F_4 generation only 2 infected individuals in one of the 8 progenies were ob-

served. From the remaining 5 F_3 progenies giving 4 to 33.3 per cent infection, 50 F_4 families were grown, and half of these were resistant and half contained smutted plants, the percentage varying from 5 to 90.9 per cent. On the basis of the general behavior of the F_2 and F_3 generations, we might expect the three groups of F_4 families—resistant, segregating, and susceptible. It is obvious, however, that a very large proportion of the F_4 families belong to the resistant group.

EXPERIMENTAL RESULTS WITH THE F_5 GENERATION

A few F_5 families, descended from 10 resistant F_3 progenies, were grown, the latter being derived from uninoculated F_2 plants. In the F_4 generation the families were also resistant, although in three cases sister progenies contained a smutted plant. Altogether, there were 24 F_5 generation families containing 447 plants, and none was infected. Thus the resistance observed in the F_3 and F_4 generations is continued through the fifth generation.

REACTION OF SOME F_3 PROGENIES TO USTILAGO LEVIS—FULGHUM

We have already mentioned the fact that both Fulghum and Black Mesdag, the parental varieties used in these crosses, are susceptible to a newly discovered race of covered smut (Reed, 1932b). No attempt to use this race in an extensive series of experiments with these hybrids has been made. However, in 1932, 24 F_3 progenies of Hybrid 31, inoculated with it, were grown. All of them contained smutted plants, the range of infection varying from 4.5 to 85.7 per cent. Neither of the parents, Fulghum or Black Mesdag, has given, as a rule, very high percentages of infection, although Fulghum has appeared to be somewhat more susceptible than Black Mesdag.

DISCUSSION AND SUMMARY

In recent years several investigators have published data on the inheritance of smut resistance in oat hybrids, and most of the literature up to 1932 has been reviewed in one of my papers (Reed, 1932a). Since then, some additional publications have appeared, including Coffman et al. (1931), Johnson (1933), Nicolaisen (1934), Schattenberg (1934), Stanton, Coffman and Tapke (1934), and Stanton, Reed and Coffman (1934). Many different oat varieties have been used in the crosses involved in the studies carried out by these investigators.

The variety Fulghum was used as one parent in some studies by Reed and Stanton (1925). Fulghum was crossed with Swedish Select, and a series of 92 F_3 progenies inoculated with *Ustilago Avenae* was grown. Fulghum

was resistant to this particular collection of loose smut, while Swedish Select was moderately susceptible. Of the 92 families grown, 25 gave no infection, 55 gave less than 40 per cent infection, and 12 were classified as susceptible. While the data were not extensive enough to determine definitely the mode of inheritance of the resistant quality, they indicated that resistance was dominant and that segregation probably occurred on the basis of a three to one ratio.

Black Mesdag has frequently been employed in hybridization experiments involving the study of the inheritance of smut resistance. It is very valuable for this purpose on account of its very great resistance to most known races of both loose and covered smut. I have used this variety in crosses with Hull-less, Silvermine, and Early Champion (Reed, 1925, 1928, 1934). Results with the F_2 generation indicated that resistance was dominant and that segregation occurred on the basis of three resistant plants to one susceptible. Data for the F_3 and later generations harmonized fairly well with this interpretation. The results were secured with definite specialized races of both loose and covered smut to which Black Mesdag was completely resistant, and Hull-less, Silvermine, and Early Champion were susceptible.

It is interesting to note that the studies on the hybrids of Fulghum and Black Mesdag in which a very different specialized race of loose smut was employed, also indicate that resistance is dominant and that segregation occurs on the basis of a three to one ratio. The data for the F_2 and F_3 generations are in harmony.

The question may be raised as to why Fulghum rarely ever gave 100 per cent infection with the particular race of loose smut used in these experiments. Two other varieties, Frazier and Kanota, which have been developed as selections from Fulghum, have given somewhat similar results. Other selections of Fulghum, however, have given higher percentages of smutted plants. Further, the variety Canadian has been inoculated at different times with this same collection of loose smut, and frequently has given 100 per cent of smutted plants.

Another problem is involved in the occurrence of occasional smutted plants in the F_3 and F_4 generations. In a few cases, completely resistant F_3 progenies gave rise to F_4 families in which a smutted plant was observed. There were also at least two cases in which a small amount of smut was found in the F_3 generation, but all of the F_4 progenies grown were resistant.

As noted above, the very susceptible F_3 progenies gave rise to F_4 families showing great variation in the amount of smut, although it might have been expected that all would be susceptible. It is true that smutted plants were found in all of these F_4 families and that most of them contained

more than 50 per cent of smutted plants. Among all the progenies, however, the percentage of infection ranged from 7.1 to 100 per cent.

All of the 24 fifth generation families grown were descended from resistant F_3 and F_4 generations. The results indicate that resistant selections through a series of generations may easily be secured. No detailed study of the inheritance of smut resistance in comparison with the inheritance of the morphological characters of the parental varieties has been made. However, the few resistant F_5 families grown combine in various ways the characters of Fulghum and Black Mesdag, especially as to color of glumes, presence or absence of awns, size and shape of the caryopsis. Some of the families are almost identical with Fulghum in morphological appearance.

Finally, it may be emphasized that the reaction of these hybrids to a specific race of loose smut has been determined. Quite different results would have been obtained if other races had been used, such as the Missouri races of loose and covered smut, to which both varieties are resistant, or the Fulghum race of covered smut, to which both are susceptible.

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The anatomy of the stem in the Lejeuneae[1]

ALEXANDER W. EVANS

(WITH EIGHT FIGURES)

INTRODUCTION

The Lejeuneae represent one of the largest and most natural groups of the Hepaticae and constitute the predominant part of the hepatic vegetation in many tropical regions. Following the example of Spruce (1885, p. 74) most writers divide them into two subgroups: the Holostipae, characterized by undivided underleaves; and the Schizostipae, characterized by bifid underleaves. In 1908 Lacouture (p. 102) separated from the Schizostipae, as a third subgroup, the "Lejeunea paradoxaux," most of the members of which are characterized by the duplication of the underleaves or by their absence. This subgroup, which may be designated the "Paradoxae," includes some of the most highly specialized and reduced of the Lejeuneae. Each of the three subgroups is further divided into a number of more or less clearly defined genera, the distinctive characters of which have been derived from the peculiarities of the leaves, underleaves, and floral organs, as well as from the general morphology of the plants.

The anatomy of the axial organs, however, has received but little attention from students of the Hepaticae. It has apparently been assumed that these organs were simple and uniform in structure and that they were therefore of slight interest to either the morphologist or the taxonomist. Such is not the case. Although the stems never attain the high degree of complexity found in the Polytrichaceae and certain other families of the Bryales (see, for example, Haberlandt, 1886, p. 392), they exhibit throughout the group a distinct differentiation into a unistratose cortex and a medulla, and these structures present a wide range of diversity in passing from the more robust genera of the Holostipae to the more delicate genera of the Schizostipae and Paradoxae. From the standpoint of the taxonomist the histological features of the stems and branches yield important characters, which supplement in many cases the characters derived from the leaves and underleaves. The histological characters, in fact, are fully as significant in the Lejeuneae as in certain other groups of the Hepaticae, in which their value is becoming more and more widely recognized. In the following account the more complex types of stem-structure will be considered first, and it is perhaps safe to assume that such types are relatively primitive and that they have given rise to the less complex types by processes of simplification and reduction.

[1] Contribution from the Osborn Botanical Laboratory.

THE ANATOMY OF THE STEM IN SELECTED SPECIES

Holostipae

BRYOPTERIS FILICINA (Swartz) Nees. According to published records *B. filicina* has a wide distribution in tropical America. The plants usually grow on the trunks of trees and show a differentiation into a prostrate caudex and spreading secondary stems. The latter are stiff and firm and maintain their rigidity whether wet or dry. They attain a length of 10–15 cm. and give off widely spreading branches at short intervals. Since the branches are normally limited in growth they give rise to distinctly pinnate branch-systems, which spread in approximately horizontal planes. The

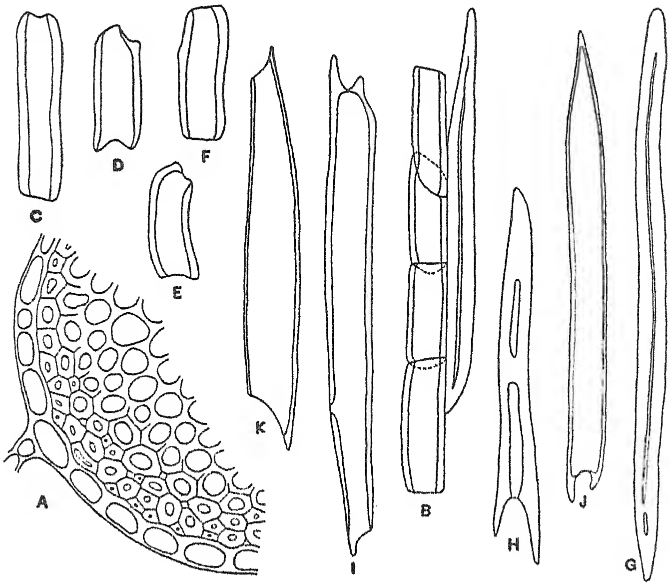


Fig. 1. *Bryopteris filicina* (Swartz) Nees. A. Cross-section of secondary stem, underleaf attached at left. B. Four cortical cells and an adjoining medullary cell. C–F. Cortical cells. G–J. Medullary cells. All, ×225.

axial organs are more or less deeply pigmented, and the stem (or main axis) may attain a width of 0.4 mm. The example illustrated by a cross-section (fig. 1, A) had a width of 0.3 mm. and a thickness of 0.25 mm., thus showing a slight dorsiventral compression. In such cross-sections the pigmentation is clearly evident, and the color varies from a pale yellow to a deep orange brown. Although all the walls are pigmented the deepest shades are found in the peripheral layers of the medulla, and the dorsal layers are

more deeply pigmented than the ventral. Toward the interior of the medulla the color rapidly becomes paler, and the walls of the cortical cells are likewise paler than those of the peripheral medullary cells.

The number of cortical cells in a cross-section varies from thirty to thirty-five, indicating approximately the number of longitudinal rows in which the cells are arranged. The cells, which appear more or less flattened, have a width of 15–25μ and a thickness of 10–12μ. The outer tangential walls are, in some cases at least, distinctly thinner than the inner tangential and radial walls, but even these rarely exceed 4μ in thickness.

The medulla is sixteen to twenty cells thick in its shorter diameter. The cells of two or three peripheral layers have strongly thickened walls and small lumina. These cells are 10–14μ in diameter, and the thickness of the wall between two lumina may be as much as 8μ. The cells in the interior have thin walls and large lumina. Their diameter, in many cases, is as much as 20μ, but their walls may be only 1–2μ thick, except for more or less distinct triangular thickenings at the angles. The transition between the peripheral and interior cells is gradual. In the walls of the peripheral layers the middle lamellae stand out clearly, not only in the walls between medullary cells, but also in the walls between medullary and cortical cells. Toward the interior the middle lamellae become less and less distinct and are soon no longer discernible. Pits can be demonstrated here and there in a cross-section but are not conspicuous.

The study of cross-sections gives only an inadequate idea of the cortical and medullary cells and of the differences between them. To show the true forms of the cells longitudinal sections are helpful, but macerated preparations are even more satisfactory. These can be easily obtained by treating fragments of stems with Schulze's maceration mixture. If the fragments are heated for a few seconds in the mixture and then washed thoroughly with water they can readily be torn apart under a dissecting microscope. In such preparations the cortical cells can be distinguished from the medullary cells by their relatively short length. This is, in most cases, between 25μ and 70μ, whereas the length of the medullary cells is between 120μ and 220μ. Speaking generally, therefore, the medullary cells are three or four times as long as the cortical cells. Figure 1, B, which represents four cortical cells in optical radial section, together with an adjoining medullary cell, brings out this relationship clearly. In figure 1, C–F, four cortical cells in surface-view are shown. It will be seen from these figures that the cortical cells are approximately rectangular in longitudinal section, with parallel sides. The longitudinal walls, whether tangential or radial, are uniformly thickened, but the end walls are thin throughout the greater part of their extent, thus allowing communication between the

cells in a longitudinal direction. The ends of the cells, in many cases, slightly overlap or develop one or two short and blunt projections.

The majority of the cells at and near the periphery of the medulla, as shown in figure 1, B, G, are in the form of short sclerenchyma fibers, tapering at each end to a sharp or blunt point. The lumina of these cells are reduced to narrow canals and may be entirely obliterated at the ends. Even in other parts of the cell, as shown in figure 1, G, the lumen may be bridged across by deposits of cell-wall substance. Deviations from the ideal fiber-like form are not infrequent. In the example shown in figure 1, H, one end is pointed and without a lumen, but the other end is broad and runs out into two slender pointed processes with an area of thin cell-wall between them. This cell, too, shows a bridge of cell-wall substance at about the middle. The cell illustrated in figure 1, I, which was situated at some little distance from the periphery, shows an area of thin cell-wall at each end. At the upper end the thick longitudinal wall extends as two short solid processes, but at the lower end the wall gradually thins out. In this cell a pit is represented in optical section on the left-hand side. Cells from the interior of the medulla, two examples of which are shown (fig. 1, J, K), are similar in form to the cell just described but have thinner walls. The cell represented in figure 1, J is pointed at one end and bears two solid projections at the other, with a thin, almost transverse area between them; but the cell represented in figure 1, K, shows a thin oblique area at each end, with a single solid point projecting beyond it. It is evident, from the examples figured, that the various types of medullary cells intergrade into one another, however different the peripheral cells may be from the interior cells. Except in the extreme fiber-like types the cells show more or less effective arrangements for the passage of liquids in a longitudinal direction. The scarcity of pits in the longitudinal walls, however, would apparently make the passage of liquids in transverse and oblique directions far more difficult. In all probability pits are more abundant in young medullary cells and become more or less filled up as the cells reach maturity.

The structure of the stem in *Bryopteris filicina* does not correspond very closely with either of the types distinguished by Herzog (1925, p. 67). It agrees with his second type, as exemplified by *Cephalozia connivens* (Dicks.) Lindb., in having a unistratose cortex, but the cortical cells differ in being relatively smaller and in having somewhat thicker walls. The medulla, moreover, is more highly differentiated than that of the *Cephalozia*, since it shows an external layer of thick-walled cells enclosing an internal core of cells with thinner walls. If the cortex were absent the stem, in cross-section at least, would resemble Herzog's first type, as exemplified by *Plagiochila asplenioides* (L.) Dumort., in which a pluristratose cor-

tex of thick-walled cells surrounds a medulla composed of thin-walled cells.

PTYCHANTHUS STRIATUS (Lehm. & Lindenb.) Nees. This widely distributed species of tropical Asia and Africa is found on both rocks and trees. It resembles *Bryopteris filicina* in being differentiated into a prostrate caudex and widely spreading secondary stems. The latter attain a length of 8–10 cm. and give rise to numerous branches, most of which are

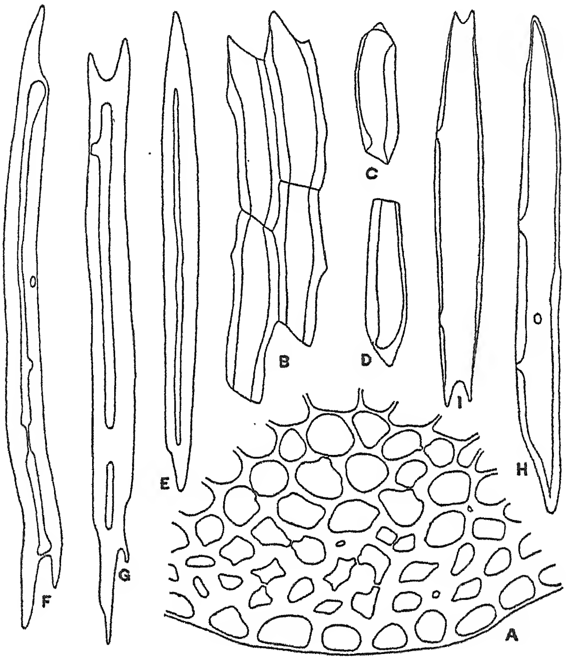


Fig. 2. *Ptychanthus striatus* (Lehm. & Lindenb.) Nees. A. Cross-section of secondary stem, ventral portion. B. Group of four cortical cells, surface-view. C, D. Cortical cells, radial view. E–I. Medullary cells. All, ×225.

sooner or later limited in their growth. In this way, much as in the *Bryopteris*, flat pinnate branch-systems are developed, the axial organs of which are firm and rigid whether wet or dry. The stem studied by the writer was about 0.45 mm. in width and 0.3–0.35 mm. in thickness. Cross-sections show a deep yellow color in the outer part, fading rather abruptly to a pale yellow or cream color in the interior.

The number of cortical cells in a cross-section (fig. 2, A) is approximately fifty, and these cells are very similar in appearance to the peripheral medullary cells, except that their external walls are thinner and

their cavities larger. The cortical cells have a rectangular outline and are 20–30μ in width by 12–16μ in thickness. The external walls are only 3–4μ thick and thus stand in rather sharp contrast to the radial walls, which are about 8μ thick.

The medulla is about sixteen cells across from top to bottom and is bounded on the outside by two or three layers of very thick-walled cells. The interior is composed of cells with much thinner walls, and the transition from the external layers to the interior is less gradual than in the *Bryopteris*. The cells at and near the periphery average about 18μ, and the thickness of the wall between two lumina may be as much as 8–10μ. The cells in the interior have about the same diameter as the peripheral cells, but their walls may be only 2–3μ thick, except for the triangular thickenings at the angles. Pits are everywhere abundant in the medulla, not only in the thick-walled peripheral layers, but also in the thin-walled interior. The middle lamellae, however, are much less distinct than in *Bryopteris filicina*, and the cortex is therefore less clearly marked off from the medulla.

Macerated preparations show that the cells of the stem are much like those of the *Bryopteris* but that they differ in a few minor details. In figure 2, B, a group of four cortical cells is represented in surface-view and in figure 2, C, D, two cortical cells in optical radial section. These figures show clearly that the radial longitudinal walls of the cells are uniformly thickened, that the outer tangential walls are thinner than those adjoining the medulla, and that the end-walls have extensive thin areas, allowing easy communication between the cells in a longitudinal direction. The ends of the cells are, in some cases, cut across transversely or obliquely but, in other cases, extend out as short pointed processes, which may be thin-walled throughout or show a deposit of cell-wall substance at the tip. These features show that the cortical cells, as in the *Bryopteris*, may overlap at their ends or be otherwise more or less firmly wedged together. Their length usually varies between 40μ and 70μ, but an occasional cell may be as much as 120μ long.

The medullary cells are mostly 150–250μ long. Those at the periphery, like the example represented in figure 2, E, are, in many cases, in the form of short sclerenchyma fibers with pointed ends. Such cells are essentially like the peripheral fibers found in the *Bryopteris*, except that their lumina tend to be a little broader. Two other cells from the peripheral region, in which the ends have developed irregular solid projections of cell-wall substance, are shown in figure 2, F, G. In figure 2, F, each end exhibits a thin area in connection with the projections, but in figure 2, G, both ends

are solid. In figure 2, F, the lumen of the cell is strongly contracted below the middle, and the wall on the right-hand side shows two partially obliterated pits. In the upper pit a deposit of cell-wall substance stretches across the opening of the canal, leaving a small cavity next to the pit-membrane; in the lower pit the deposit fills the bottom of the canal only. Figure 2, H, represents a medullary cell just inside the peripheral sheath. In this cell both ends are pointed, and the lower end is thick-walled throughout. On the left-hand side the thick cell-wall extends almost to the upper end but, on the right-hand side, thins out at about the middle. The upper end of the cell and the upper half of the right-hand side are relatively thin-walled. Three pits are visible in this cell, two in profile-view on the left-hand side and one in surface-view a short distance below the middle. In figure 2, I, a cell from the interior of the medulla is represented. The longitudinal walls of this cell are about as thick as the wall at the upper end of the cell shown in figure 2, H; each of the thin-walled ends has developed two pointed processes; and two well-marked pits are visible on the left-hand side. Pits in the longitudinal walls are apparently much more abundant in *Ptychanthus striatus* than in *Bryopteris filicina*.

STICTOLEJEUNEA KUNZEANA (Gottsche) Schiffn. In this Andean species another plant is met with in which the shoot is differentiated into a prostrate caudex and flat pinnate branch-systems. These are unusually robust and may attain a length of 20 cm. or even more. In the plant selected for study the main axis had a width of 0.35–0.4 mm. and a thickness of 0.3–0.33 mm. Although the walls of the leaf-cells are colorless or nearly so, the walls of the axial organs are distinctly pigmented with varying shades of yellow or brown. In cross-sections all the walls appear pigmented, but a deep orange–brown peripheral band stands in sharp contrast to the pale yellow or cream-colored interior. This band is four or five cells wide at top and bottom and two or three cells wide on the sides.

The morphological differences between the cortical cells and the peripheral medullary cells appear very slight in cross-section (fig. 3, A). They are both characterized by very thick walls and small cavities, and the boundaries of the cells are clearly indicated by the more deeply pigmented middle lamellae. In many of the cells the cavities are in the form of narrow slits, lying parallel with the edge of the section. The cortical cells, which number sixty to seventy in cross-sections, are mostly 12–16μ in width by 10–12μ in thickness, and the external walls often attain a thickness of 6–8μ.

The medulla is sixteen to eighteen cells thick from top to bottom. The

cells of the peripheral portion are mostly 15–20μ in diameter but may be as much as 25μ, and the wall between two cavities may be as much as 10μ thick. These cells therefore, in their transverse dimensions rival or even slightly exceed the cortical cells. The internal cells of the medulla average

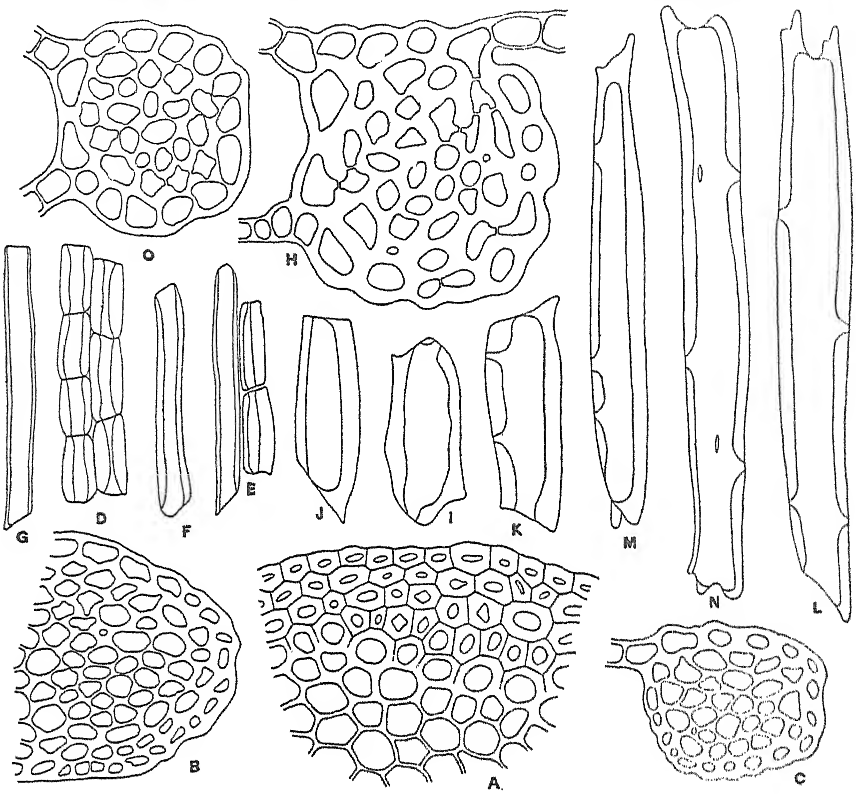


Fig. 3. A. *Stictolejeunea Kunzeana* (Gottsche) Schiffn. Cross-section of secondary stem, dorsal portion. B. *S. squamata* (Willd.) Schiffn. Cross-section of stem, lateral half. C–G. *Neurolejeunea Breutelii* (Gottsche) Evans. C. Cross-section of stem, lobe attached at left. D. Group of cortical cells, surface-view. E. Two cortical cells and an adjoining medullary cell, radial view. F, G. Medullary cells. H–N. *Omphalanthus filiformis* (Swartz) Nees. H. Cross-section of stem, lobe and lobule of leaf attached at left, lobe of another leaf at right. I–K. Cortical cells. E–N. Medullary cells. O. *Leuco-lejeuna xanthocarpa* (Lehm. & Lindenb.) Evans. Cross-section of stem, leaf attached at left. All, ×225.

about 20μ in diameter, but an occasional cell may be as much as 30μ across. The walls are only 2–3μ thick, except for the indistinct triangular thickenings at the angles. Pits are present in all parts of the medulla but are not always easy to demonstrate; in the peripheral layers they seem to be more frequent in the radial than in the tangential walls.

The axial cells of *Stictolejeunea Kunzeana* in macerated preparations are much like those of *Bryopteris filicina* and *Ptychanthus striatus*. The distinctions between the cortical cells and the peripheral medullary cells, however, are less pronounced. The cortical cells, for example, although only 30μ long in some cases, are usually 60–80μ long and may attain a length of 100μ. Since the length of the medullary cells is mostly between 140μ and 240μ, the shortest medullary cells are not much longer than the longest cortical cells.

STICTOLEJEUNEA SQUAMATA (Willd.) Schiffn. The second species of *Stictolejeunea* to be considered is widely distributed in tropical America and grows on both trees and rocks. Although the plants form irregularly pinnate branch-systems, comparable with those of *S. Kunzeana*, there is no differentiation into a prostrate caudex and spreading secondary stems. The branch-systems, on the contrary, are produced by the branching of the prostrate primary stems and are themselves prostrate or very slightly ascending. The plants are therefore less exposed to the dangers of mechanical injury and desiccation than are those of *S. Kunzeana*. The stems of *S. squamata* are about 0.2 mm. in width by 0.15 mm. in thickness. The pigmentation of the stem, as seen in cross-sections, is less pronounced than in *S. Kunzeana*, the contrast in color between the orange yellow peripheral layer and the paler yellow interior is less marked, and the change from one to the other is more gradual. A cross-section (fig. 3, B) brings out scarcely any morphological differences between the cortical cells and the peripheral medullary cells: both are characterized by uniformly thickened walls and more or less reduced lumina. The cortical cells, of which thirty-five to forty are visible, measure 10–20μ in width by 8–15μ in thickness, and the cells on the dorsal surface are distinctly larger than those on the ventral surface. The external walls are mostly 4–6μ thick.

The medulla is only eight or nine cells thick in its shorter diameter, and the peripheral cells with uniformly thickened walls occupy only one or two layers. The next layers are transitional in character, and the internal cells are distinguished from the peripheral cells by their much thinner walls, with more or less distinct triangular thickenings at the angles. The medullary cells average about 15μ in diameter, but the largest are 20μ wide. Some of the medullary cells, therefore, are larger in their transverse dimensions than some of the cortical cells.

NEUROLEJEUNEA BREUTELII (Gottsche) Evans. The species of *Neurolejeunea* are smaller and less definite in habit than any of the forms so far discussed. In the species under consideration the plants have a deep olive

green or olive brown color and grow in loose tufts on rocks and trees. The individual stems are mostly 3–5 cm. in length and give off branches sparingly and irregularly. In the plant examined the stem had a width of about 0.15 mm. and a thickness of about 0.12 mm., but more slender stems are not infrequent. A brown pigmentation of all the cell-walls is shown in cross-sections, and the difference in shade between the darker peripheral portion and the paler interior portion is very slight. The morphological differences between the cortex and medulla, as brought out by cross-sections (fig. 3, C), are by no means striking. The cortical cells, which number about eighteen, measure 10–20μ in width by 10–15μ in thickness, and their external walls are about 4μ thick.

The medulla, in most cases, is only five cells across from top to bottom. The cells composing it average about 12μ in diameter, although an occasional cell may be as much as 20μ in width. The walls are mostly only 2–3μ thick but show indistinct triangular thickenings at their angles. Since the walls of the peripheral cells are only a little thicker than those of the interior cells, the medulla is not differentiated into a thick-walled sheath surrounding a thin-walled core. Pits and middle lamellae are difficult to demonstrate.

Individual cells or groups of cells obtained by maceration are represented in figure 3, D–G, and indicate that the cell-differentiation is relatively slight. Figure 3, D, shows a group of cortical cells which are still in contact. The thick longitudinal radial walls appear in optical section, and the transverse or slightly oblique end-walls have extensive thin areas. In figure 3, E, two cortical cells in optical radial section and an adjoining medullary cell are shown in their relative positions. The cortical cells bring out the fact that the outer wall is thicker than the inner, and the lower cell shows a short pointed projection of cell-wall substance. The medullary cells, represented in figure 3, F, G, are several times as long as broad and are characterized by their more or less thickened longitudinal walls and thin end-walls. The latter, which may be transverse or oblique, run out, in some cases, into short, bluntly pointed processes. Apparently none of the cells have the form of sclerenchyma fibers. The cortical cells are mostly 25–50μ in length and the medullary cells, 90–120μ.

OMPHALANTHUS FILIFORMIS (Swartz) Nees. Few species are more abundant in the lower mountains of the American tropics than *O. filiformis*. The plants form loose, yellowish green tufts on various substrata and assume, in most cases, an ascending or suberect position. The main stems are 5–10 cm. in length and give off branches sparingly and irregularly. Cross-sections (fig. 3, H), which are approximately circular,

have a diameter of about 0.15 mm. and show a uniform orange-yellow pigmentation throughout. At first sight the sections seem to be undifferentiated into cortex and medulla, since all the cells have uniformly thickened walls. Closer inspection, however, shows that the transverse dimensions of the cortical cells are a little larger than those of the medullary cells, and the study of macerated tissues brings out other and more important distinctions. The cortical cells, which number twelve to fifteen in a cross-section, bulge outward and give the periphery a crenulate appearance. They are mostly 20–30μ in width by 20–25μ in thickness, and the external walls, in many cases, are 8–12μ thick. In some of the radial walls pits can be demonstrated, as shown in the lower part of figure 3, H.

The medulla is mostly six or seven cells across, and there is no distinction between the peripheral and internal portions. The cells average about 16μ in diameter, and their walls are usually 8–12μ thick. Although the middle lamellae are scarcely distinguishable, pits are conspicuous and can be demonstrated, not only in the walls between medullary cells, but also in the walls between medullary and cortical cells. Ample provision, therefore, is apparently present for communication between cells in transverse directions.

The medullary cells, in macerated preparations, are seen to be three or four times as long as the cortical cells. The latter are mostly 50–80μ in length but may be as much as 100μ. Figure 3, I, represents a cortical cell in surface-view; figure 3, J, K, two cortical cells in optical radial section. The radial walls of the cell shown in figure 3, I, are strongly thickened and show no pits, but the upper end-wall shows two thin areas and the lower end-wall one. In all probability the upper end of the cell abutted against two cells belonging to different rows, and the thin areas afforded communication with those cells. Similar relationships, in some cases, can be demonstrated between cells on intact stems. The short pointed projections of cell-wall substance at the ends of the cell doubtless served to increase the firmness of the union with adjoining cells. In the cells shown in figure 3, J, K, the walls on the right-hand side represent the outer tangential walls. In figure 3, J, this wall is distinctly thicker than the inner tangential wall, which is apparently destitute of pits; in figure 3, K, on the contrary, the two tangential walls are subequal in thickness and the inner wall shows two pits. The oblique end of the cell shown in figure 3, J, and the two oblique ends of the cell shown in figure 3, K, indicate more or less overlapping.

The medullary cells are apparently never developed in the form of sclerenchyma fibers with pointed ends. The characteristic examples repre-

sented in figure 3, L–N, show that the ends are broad, although they may be either transverse or oblique. All of the cells figured show at each end from one to three short processes of cell-wall substance, and the processes at the upper end of figure 3, L, have given off secondary processes. Except in the case of the upper end of the cell shown in figure 3, M, where the wall is uniformly thickened, each end shows one or two thin areas. The thick side-walls of the cells figured show a number of pits in profile-view, and figure 3, N, shows two pits in surface-view. These pits are in the form of narrow ellipses running longitudinally and are similar to the pits found in the bast-fibers of *Antitrichia curtipendula* (Hedw.) Brid., as figured by Haberlandt (1886, *pl. 21, f. 11*). The medullary cells of *Omphalanthus filiformis* are mostly 240–360μ in length and thus tend to be longer than in any of the preceding forms.

LEUCOLEJEUNEA XANTHOCARPA (Lehm. & Lindenb.) Evans. The pale glaucous green plants of *L. xanthocarpa* grow on the bark of trees and form thin depressed mats. The species has an unusually wide distribution and is found not only in the tropical and subtropical portions of North and South America but also in Africa and the East Indies. The prostrate stems, which are subterete, branch irregularly and are mostly 2–5 cm. in length by 0.1–0.15 mm. in diameter. Cross-sections (fig. 3, O) are, in general, much like those of *Omphalanthus filiformis*. The cell-walls, for example, although of a pale yellow color, are uniformly pigmented throughout, the cells are everywhere thick-walled; and the visible distinctions between the cortical and medullary cells are relatively slight. The cortical cells, which number about fifteen, are 15–25μ in tangential width by 15–20μ in radial width, and their external walls are 4–8μ thick. The periphery of a section scarcely appears crenulate, although some of the cells bulge slightly. The medulla is four or five cells across, the medullary cells average about 14μ in diameter, and the walls are 6–8μ thick. The thickenings, however, owing to the frequency of pits, present the appearance of being brought about by the coalescence of trigones. The pits can be demonstrated, as in the *Omphalanthus*, not only in the walls between medullary cells, but also in the walls between medullary and cortical cells and in the radial walls between cortical cells.

ARCHILEJEUNEA SPRUCEANA Steph. The species of *Archilejeunea* have the shoot differentiated into a prostrate primary stem and spreading secondary stems. The latter, which are relatively short, are either simple or sparingly and irregularly branched. The plants do not form, therefore, complicated pinnate branch-systems like those found in *Bryopteris*, *Ptychanthus*, and *Stictolejeunea Kunzeana*. The species here considered is

abundant in eastern South America and grows on the bark of trees. The plants are reddish green or brownish green, and the secondary stems have a length of 2.5–5 cm. and a diameter of about 0.15 mm. In spite of the difference in habit between *A. Spruceana* and *Leucolejeunea xanthocarpa*, the structure of the stem is much the same, although the contrast in size between the cortical and medullary cells is a little more pronounced in the *Archilejeunea*. Cross-sections show a pigmentation with pale brownish yellow throughout, with but slight variation in shade. The cortical cells

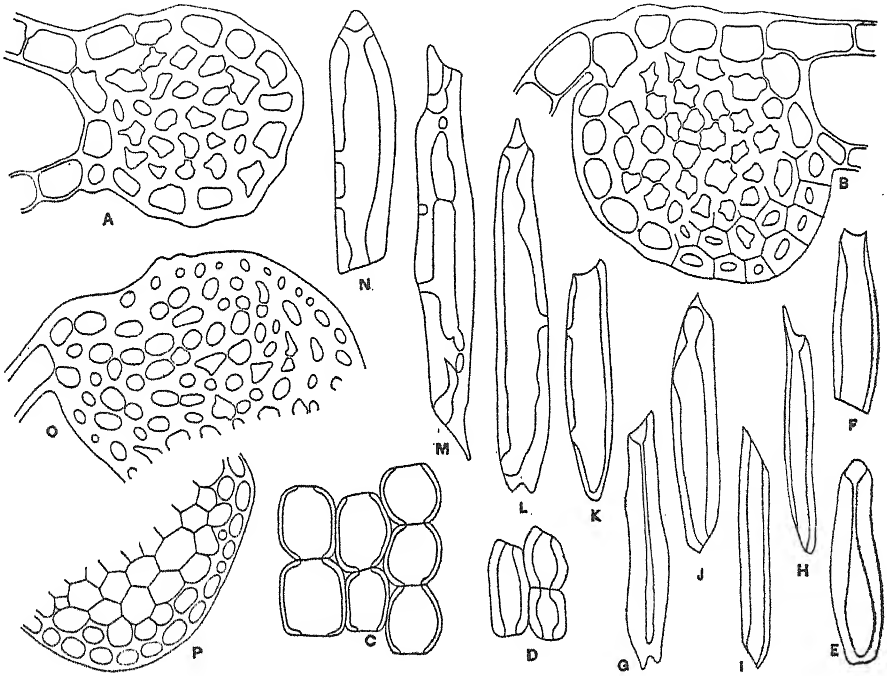


Fig. 4. A. *Archilejeunea Spruceana* Steph. Cross-section of stem, leaf attached at left. B–N. *Mastigolejeunea auriculata* (Wils. & Hook.) Schiffn. B. Cross-section of stem, lobe and lobule of leaf attached at right, lobe of another leaf at left. C, D. Groups of cortical cells. E–N. Medullary cells. O, P. *Thysananthus amazonicus* (Spruce) Schiffn. O. Cross-section of mature stem, lobe attached at left. P. Cross-section of young stem, ventral portion. All, ×225.

(fig. 4, A) number about fifteen and measure 20–25μ in width by 15–20μ in thickness. The external walls, in most cases, are 4–6μ thick but may be as much as 8μ thick. The medullary cells average about 13μ in diameter, and the thickenings of the cell-walls, together with the distribution of the pits, are essentially the same as in the *Leucolejeunea*.

MASTIGOLEJEUNEA AURICULATA (Wils. & Hook.) Schiffn. The genus *Mastigolejeunea* agrees with the preceding genus in having the shoot differentiated into a primary caudex attached to the substratum and secondary stems. The latter spread very slightly, and the plants in consequence form depressed mats. The pigmentation is sometimes so pronounced that both leaves and axial organs appear almost black when dry. The stems branch irregularly and the branches, in many cases, give rise to secondary and tertiary branches, all essentially like the stem. The range of the common *M. auriculata*, which grows on trees, logs, and rocks, extends from Florida to Louisiana and southward through the tropics of North and South America. The stems are mostly 3–5 cm. in length by 0.15–0.18 mm. in diameter, and the cell-walls in cross-section are pigmented throughout with varying shades of yellow or brown. Usually, however, a dark brown band one or two cells wide can be distinguished along the ventral edge of the section and a paler brown, more indistinct band along the dorsal edge.

The cortex, as seen in a cross-section (fig. 4, B), is clearly differentiated from the medulla. The cortical cells, which number fifteen to eighteen, measure 15–25μ in width by 15–20μ in thickness, and the dorsal cells tend to be larger than the ventral. The cells show considerable variation, not only in size, but also in the thickness of their walls. The external walls of the dorsal and lateral cells in the figure, for example, are 4–6μ thick, and the cavities are fairly large; but a group of ventral cells is shown with walls 8μ thick and much smaller cavities, which tend to be slit-like. Similar cells are present in most cross-sections. They are normally ventral in position but may extend for variable distances up the sides. The thick walls are further characterized by their distinct middle lamellae, which are darker than the other layers.

The medulla is mostly six or seven cells across and is composed of thick-walled cells having an average diameter of about 13μ. Adjoining the cortical cells with the thickest walls there is usually a group of similar medullary cells with uniformly thickened walls and distinct middle lamellae. The other medullary cells have walls almost as thick but the thickenings, owing to the presence of numerous pits, present the appearance of being formed by the coalescence of robust trigones. The thickness of the wall between two medullary cells is usually between 6μ and 8μ but may be as much as 10μ.

Macerated preparations of the stems bring out a few additional features of the component cells. The cortical cells, two groups of which are represented in surface-view, are mostly 25–60μ in length. The seven partially separated cells shown in figure 4, C, have relatively thin radial

walls, and the three cells shown in figure 4, D, relatively thick radial walls. The cells in both groups have thin end-walls and are destitute of pits in the radial walls. The ends of the cells show little evidence of overlapping. The medullary cells are mostly 70–200μ in length and show a tendency to be shorter in the vicinity of the cortex than in the interior. Figure 4, E–I, represent cells from a more or less peripheral position. These cells have uniformly thickened longitudinal walls and, in most of the examples, thin end-walls. In some cases the broad, transverse or oblique ends lack outgrowths of any kind, but the cell shown in figure 4, G, has two short solid processes at the lower end, and the cell shown in figure 4, F, has two thin-walled protuberances at the upper end. Apparently the longitudinal walls are destitute of pits. The cells represented in figure 4, J–N, are from the interior of the medulla. These cells are mostly longer than the peripheral cells and each one shows one or more pits in optical section; otherwise they present no distinctive features. The old cell shown in figure 4, M, has the lumen bridged across in several places by thin films of cell-wall substance, and one of the pit-canals on the left-hand side has been filled up in the outer part, leaving a small cavity next to the pit-membrane. A similar condition has been noted in *Ptychanthus striatus*.

THYSANANTHUS AMAZONICUS (Spruce) Schiffn. The genus *Thysananthus* is closely related to *Mastigolejeunea* and agrees with it in general habit. In other words the plants form depressed mats and are differentiated into prostrate primary stems, adherent to the substratum, and free, irregularly branched secondary stems. The genus, although largely paleotropic, has a few representatives in tropical America; and *T. amazonicus*, according to Spruce, is perhaps the most abundant of all the Lejeuneae along the Amazon and its tributaries. The plants are brownish, except the young bright green tips, and grow on the branches and trunks of shrubs and small trees. The secondary stems are mostly 3–8 cm. in length by about 0.15 mm. in diameter, and cross-sections show an orange brown pigmentation, which is uniform except for the indistinct and slightly darker middle lamellae. These are not represented in the section illustrated (fig. 4, O). The cortex, as shown in the figure, is not sharply demarcated from the medulla. It is composed of thirty to thirty-three rows of thick-walled cells, 10–20μ in width by 10–15μ in thickness, and the external walls are mostly 4–7μ thick. The medulla, which is eight to ten cells across is composed of thick-walled cells about 13μ in diameter. The walls, in many cases, are as much as 6–8μ thick, but the cell-cavities are distinctly larger than those of the cortical cells. The medulla, in consequence, appears a little more open than the cortex. Owing to the rather numerous

pits in the medulla, the thickenings of the walls, in some cases at least, seem to be formed by the coalescence of trigones, much as in *Leucolejeunea xanthocarpa* and *Archilejeunea Spruceana*.

In young stems the cortex is more sharply marked off from the medulla than in mature stems. A cross-section (fig. 4, P) shows this clearly and indicates further that the differentiation of the tissues progresses centripetally from the periphery toward the interior. In the section represented the walls of the cortical cells have already received deposits of thickening, although the process has not yet come to an end. The medulla, however, is still composed of thin-walled cells, with the exception of the peripheral layer, and even here the process of thickening is still in its early stages.

BRACHIOLEJEUNEA INSULARIS Evans. In the species so far considered the disparity in size between the cortical and medullary cells, as seen in cross-sections of stems, has been comparatively slight. In most cases, to be sure, the cortical cells have been a little larger than the adjoining medullary cells, but they have been approached or even equaled in size by some or all of the interior medullary cells. In other cases, where the medullary cells have been uniform throughout, there has been almost no difference in size between the cortical and medullary cells; and, in a very few cases, the cortical cells have been a little smaller than the medullary cells. In *Brachiolejeunea insularis* and in a few other Holostipae now to be discussed, the cortical cells, in cross-section, are distinctly larger than the medullary cells. The stems of these species agree in most respects with the first type of stem-structure distinguished by Herzog (1925, p. 67), who looks upon the large-celled cortex as a water-storage tissue. It probably plays an important part also in photosynthetic processes, as suggested by Buch (1932, p. 57, footnote).

The genus *Brachiolejeunea* has numerous representatives in tropical regions throughout the world, and a few species are found in subtropical or even temperate localities. The plants, which are usually deeply pigmented, form depressed mats, and the prostrate stems are irregularly branched. According to our present knowledge *B. insularis* is restricted to the West Indies, where it grows on either trees or logs. The stems, in well-developed specimens, are 6–10 cm. long and about 0.16 mm. in diameter. In cross-sections the cell-walls everywhere have a uniform pale yellow or cream color, with the frequent exception of the outermost walls, which may be a pale yellowish brown. The cortical cells (fig. 5, A), fourteen to sixteen in number, are rectangular to subquadrate and measure 25–40μ in width and thickness. They are distinguished by their large cavities and

relatively thin walls, those on the outside being only 1–3μ in thickness. The medulla is six or seven cells across, and the medullary cells average about 17μ in diameter. The walls of these cells, which are essentially alike throughout the section, are about 4μ thick, with more pronounced thickenings at the angles, and an occasional pit can be demonstrated.

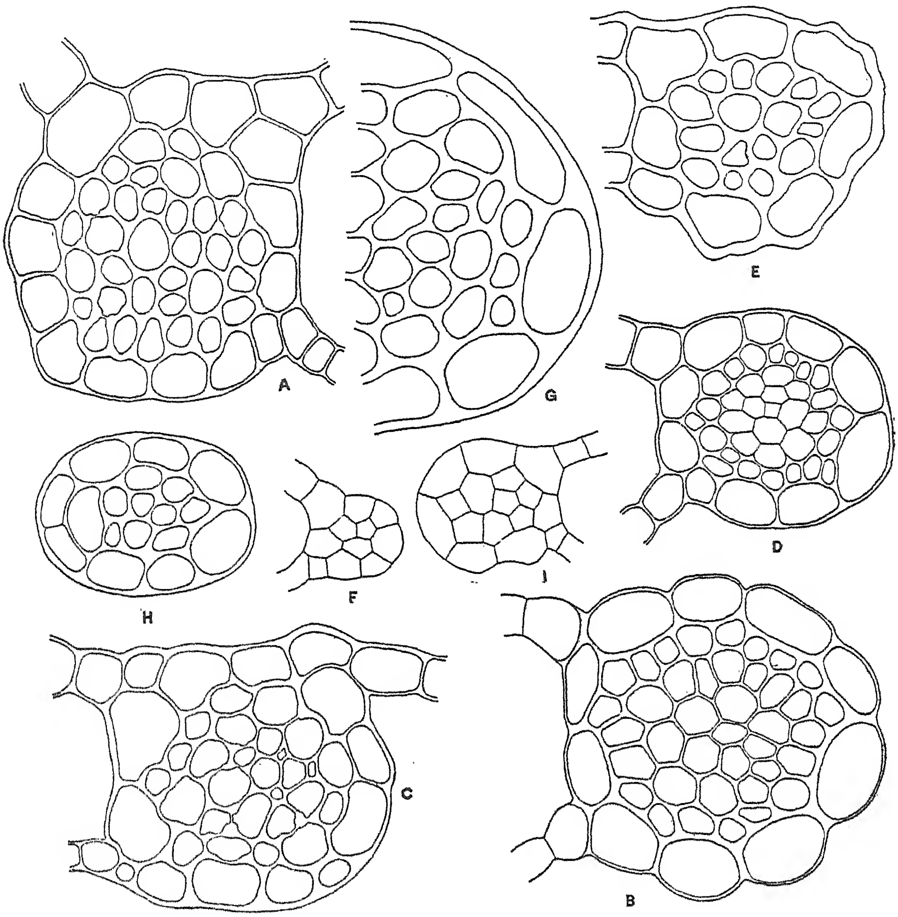


Fig. 5. Cross-sections. A. Stem of *Brachiolejeunea insularis* Evans, leaf attached at right, lobe of another leaf at left. B. Stem of *Dicranolejeunea axillaris* (Nees and Mont.) Schiffn., leaf attached at left. C. Stem of *Caudalejeuna Lehmanniana* (Gottsche) Evans, leaf attached at left, lobe of another leaf at right. D. Stem of *Odontolejeunea lunulata*, leaf attached at left. E, F. *Anoplolejeunea conferta* (Meissn.) Evans. E. Stem, leaf attached at left. F. Microphyllous branch, leaf attached at left. G. Stem of *Cyclolejeunea chitonia* (Tayl.) Evans, lateral half. H. Stem of *C. peruviana* (Lehm. and Lindenb.) Evans. I. Stem of *C. convexistipa* (Lehm. and Lindenb.) Evans, leaf attached at right. All, ×225.

DICRANOLEJEUNEA AXILLARIS (Nees & Mont.) Schiffn. The genus *Dicranolejeunea* is widely distributed in the tropical regions of both Hemispheres. In some of the species the plants are prostrate throughout; in others a differentiation into a prostrate primary stem and spreading secondary stems is met with. The species under consideration, which is found in many parts of North and South America, belongs in the latter category. The plants form loose tufts, usually on the branches of trees, and are yellowish brown in color. The secondary stems, which branch irregularly, attain in many examples a length of 5–10 cm. and are about 0.15 mm. in diameter. Cross-sections are pale yellowish throughout, but the walls of the peripheral medullary cells are a shade darker than those of the other cells. The cortical cells, which number ten to fourteen in cross-section (fig. 5, B), measure 30–60μ in width by 20–30μ in thickness. The radial walls of these cells are about 4μ thick, but the outer walls are scarcely 2μ thick. The latter bulge more or less and thus give the periphery of the section a crenulate appearance. The medulla is six or seven cells from top to bottom and is bounded on the outside by a single layer of cells with somewhat thicker walls. The succeeding cells have thinner walls and the interior cells have still thinner walls. The medullary cells average about 17μ in diameter and show few or no pits, even in the peripheral layer.

CAUDALEJEUNEA LEHMANNIANA (Gottsche) Evans. Although the genus *Caudalejeunea* has several species in the tropics of the Old World, it is apparently represented in the New World by a single species, the variable *C. Lehmanniana*. The known range of this species extends from Brazil to the West Indies and Mexico, with an extension into subtropical Florida. The bright or pale green plants form loose tufts on the branches and twigs of trees and shrubs and are differentiated into prostrate primary stems, closely attached to the substratum, and spreading secondary stems. The latter, which are simple or sparingly branched, are mostly 2–3 cm. in length and 0.15 mm. or a little less in diameter. In cross-sections the cell-walls have a pale cream color, indicating an almost complete lack of pigmentation. The cortical cells (fig. 5, C), about twelve of which are present in each section, are mostly 30–40μ in width by 20–30μ in thickness. Their walls are slightly thickened, up to perhaps 4μ, but in many cases the radial and inner tangential walls show thin places. The medulla is five or six cells across, and the medullary cells average about 18μ in diameter. The walls of these cells are nearly or quite as thick as those of the cortical cells, at least in well-developed stems, but the thickenings at the angles of the cells are more pronounced than along the sides. The wall-

thickenings, in fact, give the effect of coalescent trigones, except where pits are present.

ODONTOLEJEUNEA LUNULATA (Web.) Schiffn. Although most of the preceding species have been epiphytes, they have grown on the trunks or branches of trees or shrubs. Many of the *Odontolejeuneae*, however, are strictly epiphyllous in habit and grow on the upper surface of leaves. They are, in fact, among the largest and most conspicuous of the epiphyllous Lejeuneae. The genus has a few representatives in Africa but is most at home in the American tropics, and the range of the common *O. lunulata* extends from Mexico and the West Indies into Brazil. The plants have a brownish or yellowish green color and grow closely appressed to the substratum, where they form flat patches, sometimes of considerable extent. The stems branch irregularly and are mostly 2–5 cm. in length by 0.15 mm. or a little less in diameter. Cross-sections are very pale grayish brown and show about twelve cortical cells (fig. 5, D). The latter are 25–35μ in width by 20–30μ in thickness, and the enclosed medulla, which is six or seven cells across, is composed of cells averaging about 13μ in diameter. The walls of the peripheral layer of medullary cells are slightly and uniformly thickened, but their thickness rarely exceeds 4μ. The radial walls of the cortical cells and the walls of the interior medullary cells are thin, but the outer walls of the cortical cells (at least in some cases) equal the walls of the peripheral medullary cells in thickness. Although the stem-structure of *O. lunulata* agrees in a general way with that of *Brachiolejeunea insularis*, *Dicranolejeunea axillaris*, and *Caudalejeunea Lehmanniana*, it is more delicate, owing to the thinner cell-walls. This evidence of reduction is probably associated with the epiphyllous habit, and it will be shown below that the epiphyllous Lejeuneae include some of the most reduced and simplified types of structure to be found in the entire group.

ANOPLOLEJEUNEA CONFERTA (Meissn.) Evans. The genus *Anoplolejeunea* is confined to the American tropics and is composed of very few species. The plant under consideration forms depressed green mats on the bark of trees and has an extensive range in both North and South America. The prostrate stems, which branch irregularly, are mostly 3–5 cm. in length and have a diameter of 0.12–0.17 mm. Some of the branches cling to the substratum and agree with the stem in having large leaves, but others are ascending and microphyllous. The stems show a pale and uniform brownish yellow pigmentation of the cell-walls in cross-sections. The cortical cells, as in the four preceding species, are distinctly larger than the medullary cells. Instead of being arranged, however, in ten to sixteen longitudinal rows, they are arranged in seven longitudinal rows. Of these

rows two are ventral in position, two on each side lateral and one dorsal. The illustration (fig. 5, E) shows the seven rows clearly in cross-section, but an additional cell is present on the left-hand side, marking the place of attachment of a lobule. The arrangement of the cortical cells in seven longitudinal rows and the distribution of these rows around the stem in the manner just described are unusual in the Holostipae but are found with few exceptions throughout the Schizostipae and also in the genera of the Paradoxae with underleaves. The significance of this arrangement and particularly of the dorsal row of cells will be considered later, in connection with the development of the stem.

The cortical cells of the *Anoplolejeunea* measure 40–50μ in width by 25–35μ in thickness, and some of the cells bulge slightly, thus giving the section an irregular contour. The walls are uniformly thickened, and the external tangential walls have a thickness of 6–8μ. The medulla is about four cells across, and the medullary cells have an average diameter of about 20μ. Their walls may be as much as 6μ thick, and the triangular thickenings at the angles are more or less distinct. The section figured does not show pits clearly, but these structures can occasionally be demonstrated, not only in the walls between medullary cells, but also in the walls between medullary and cortical cells.

The microphyllous branches are much more slender than the stems and branches with normal leaves and measure scarcely 0.05 mm. in diameter. Although seven rows of cortical cells are present, just as in the stem, the medulla is greatly reduced, and only three or four cells appear in cross-sections. When only three cells are present, as in the section shown (fig. 5, F), one is ventral in position and two dorsilateral, with the dorsal cortical cell fitting in between them. The cortical cells are 15–20μ in width and thickness and the medullary cells about 10μ in diameter. All the walls are thin, except for the occasional presence of minute triangular thickenings at the angles of the medullary cells.

Schizostipae

CYCLOLEJEUNEA CHITONIA (Tayl.) Evans. The genus *Cyclolejeunea* is here placed among the Schizostipae, in spite of the fact that the underleaves, at least in certain species, may be undivided. The genus is predominantly neotropical, but two species from Java have recently been assigned to it. In the West Indian *C. chitonia*, the first species to be considered, the plants form depressed mats of an olive green or brownish color on the bark of trees or on logs. The prostrate stems branch irregularly and are mostly 2–5 cm. in length by about 0.25 mm. in diameter. Cross-sections show a pale brownish yellow pigmentation, with little variation

in shade. About twelve cortical cells appear in each section, and these cells, which are unusually large, measure 40–60μ in width by 25–40μ in thickness (fig. 5, G). The outer walls are 8–10μ thick; the radial walls are a little thinner, and some of them show more or less distinct pits. The medulla, which is seven or eight cells across, is composed of cells about 20μ in diameter. The walls of the medullary cells are all thickened, but a gradual decrease in thickness is apparent in passing from the peripheral layers, where the walls are 6-8μ thick, to the interior, where the walls are only 2–4μ thick, except at the angles of the cells. Pits can be demonstrated here and there in the medulla.

CYCLOLEJEUNEA PERUVIANA (Lehm. & Lindenb.) Evans. The plants of *C. peruviana* are epiphyllous in habit and form irregular reddish brown patches. The species is abundant in the valley of the Amazon and adjoining regions and ascends into the foothills. It is frequently associated with *Odontolejeunea lunulata* and other *Odontolejeuneae* and rivals them in size. The stems, which cling closely to the substratum, branch irregularly and are mostly 3–5 cm. in length. They measure 0.11–0.14 mm. in width and 0.08–0.1 mm. in thickness, thus showing a slight dorsiventral compression. Cross-sections are of a uniform pale yellow color and normally have seven cortical cells, just as in *Anoplolejeunea conferta*, but in the section illustrated (fig. 5, H) the lower lateral cell on the left seems to have undergone a division by means of a thin radial wall. This wall, however, is really oblique and separates two cells of the same longitudinal row. The cortical cells are 30–40μ in width by 20–30μ in thickness and have walls about 6μ thick, with thinner areas in the radial walls. The medulla, in contrast of that of the more robust *C. chitonia*, is only three or four cells across. The cells average about 15μ in diameter, and their walls are about as thick as those of the cortical cells.

CYCLOLEJEUNEA CONVEXISTIPA (Lehm. & Lindenb.) Evans. The range of this species, which is perhaps the most abundant of all the epiphyllous Lejeuneae, includes the greater part of tropical America. The plants, which are more delicate than those of *C. peruviana*, form irregular pale green patches, and the cell-walls are scarcely if at all pigmented. The prostrate stems are mostly 1–2 cm. in length by 0.08 mm. in diameter and branch copiously and irregularly. Some of the branches are much like the stem, but the gemmiparous branches, which are ascending to suberect, bear modified leaves and underleaves. The cortical cells (fig. 5, I) are definitely in seven longitudinal rows and measure 25–35μ in width by 15–20μ in thickness. The medulla is three or four cells across and is composed of cells av-

eraging about 11μ in diameter. All the cell-walls are thin, except in some cases those of the cortical cells, which may be slightly thickened.

POTAMOLEJEUNEA ORINOCENSIS Steph. This aquatic species is one of the very few Schizostipae known to the writer in which the cortical cells are arranged in more than seven longitudinal rows. The pale green plants

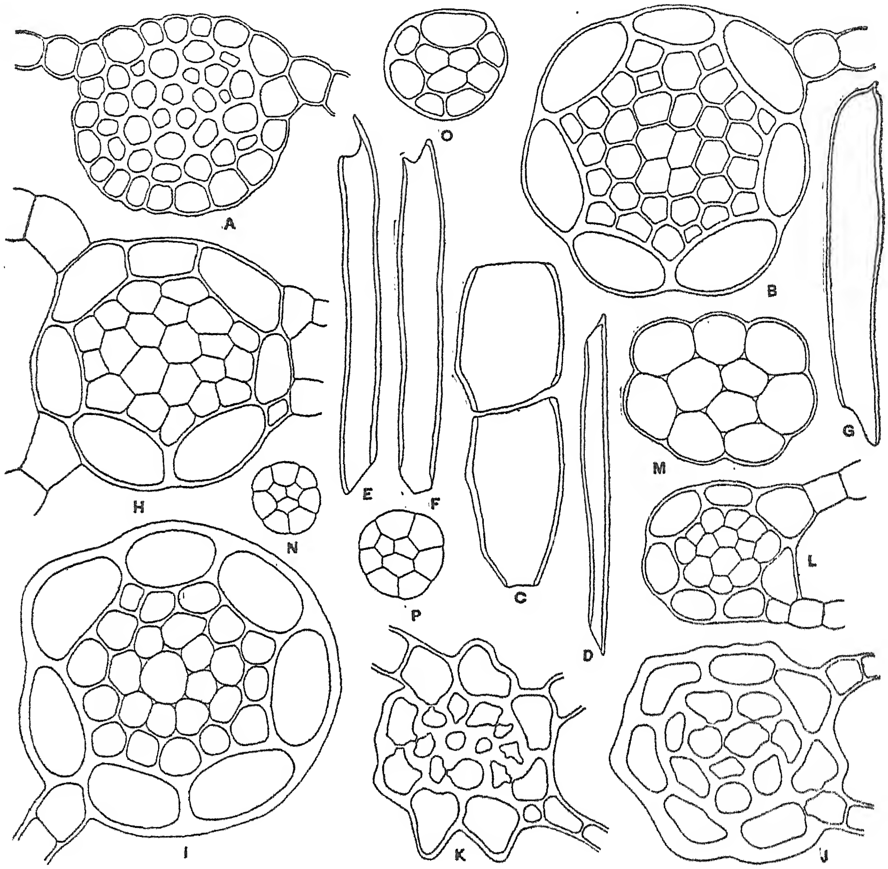


Fig. 6. Cross-sections of stems, except C–G. A. *Potamolejeunea orinocensis* Steph., a lobe attached on each side. B–G. *Taxilejeunea pterogonia* (Lehm. and Lindenb.) Schiffn. B. Lobe attached at right. C. Two cortical cells. D–G. Medullary cells. H. *Hygrolejeunea cerina* (Lehm. and Lindenb.) Schiffn., leaf attached at left. I. *Cystolejeunea lineata* (Lehm. and Lindenb.) Evans, underleaf attached at left. J. *Euosmolejeunea trifaria* (Nees) Schiffn., leaf attached at right. K. *Pycnolejeunea macroloba* (Mont.) Schiffn., leaf attached at right and lobe of another leaf at left. *L. Lejeunea flava* (Swartz) Nees, leaf attached at right. M. *L. inundata* Spruce. N. *Microlejeunea bullata* (Tayl.) Evans. O. *Drepanolejeunea inchoata* (Meissn.) Schiffn. *P. Leptolejeunea elliptica* (Lehm. and Lindenb.) Schiffn. All, $\times 225$.

form loose tufts on moist rocks in the lowlands of tropical South America and are often completely submerged. The stems, which are about 0.12 mm. in diameter, give off branches at fairly regular intervals and may attain, according to Stephani, a length of 12 cm. Cross-sections are colorless or a very pale cream color and cut through about twenty cortical cells, which measure 10–20μ in width and thickness (fig. 6, A). The thin outer walls of these cells bulge more or less and give the section a crenulate contour. The radial walls also are thin toward the outside but thicken slightly toward the medulla. The cells of the latter are in about six layers and average about 16μ in diameter. Their walls are about 4μ thick, and the thickening is uniform, except for the fact that the cavities are rounded. Pits are difficult to demonstrate, but the middle lamellae show clearly in many of the walls.

TAXILEJEUNEA PTEROGONIA (Lehm. & Lindenb.) Schiffn. In this widely distributed species of tropical America, the differentiation of the stem-tissues and the arrangement of the cortical cells in seven longitudinal rows are exhibited with almost diagrammatic distinctness. The plants are pale green and form loose mats on rocks and firm soil. The stems are mostly 3–4 cm. long by 0.15–0.2 mm. in diameter and give off a few long vegetative branches in addition to the short sexual branches. Cross-sections show a complete lack of pigmentation in the cell-walls. The large cortical cells (fig. 6, B) are 40–60μ in width by 20–30μ in thickness, and their walls are about 4μ thick. The bounding walls bulge outward and the inner tangential walls bulge inward. The circumference of the section, in consequence, appears more or less crenulate and the periphery of the medulla more or less stellate. The latter is seven or eight cells across, and the medullary cells average about 14μ in diameter. The walls between the cortex and medulla are about 6μ thick and those of the peripheral medullary cells about 4μ thick. In passing inward the walls become thinner and thinner, and the interior cells are thin-walled. Neither middle lamellae nor pits show in cross-sections.

It is perhaps worthy of note that a vertical line passing through the dorsal cortical cell and between the two ventral cortical cells divides the section into symmetrical halves. This indicates that the stem is a bilaterally symmetrical organ with respect to a median vertical plane of symmetry, if a horizontal position is assumed. The vertical line, however, is not the only axis of symmetry. A line passing through any cortical cell and between the opposite pair of cortical cells would likewise be an axis of symmetry. Since seven cortical cells are present the section would have

seven axes of symmetry and the stem seven planes of symmetry. This indicates that the stem, considered by itself, is really a radial organ.

Macerated preparations show that the cortical and medullary cells, in their essential features, are in agreement with those of some of the Holostipae already considered. The cortical cells (fig. 6, C) are mostly 50–90μ long and fit together with blunt angles. In some of the cells the ends overlap slightly or give off one or two short and blunt projections, but such features are not strongly in evidence. The end walls remain thin; but the longitudinal walls, as already noted in the cross-sections, are uniformly thickened, and pits are conspicuous by their absence. In figure 6, D–G, four medullary cells are represented, and the cell shown in figure 6, G, is nearer the interior than the others. These cells are mostly 150–190μ in length, their end walls are mostly thin, and their longitudinal walls uniformly thickened. The ends of the cells vary from transverse to oblique; and, in some cases, one or two short projections are present. Even in the thickest longitudinal walls no pits are visible.

HYGROLEJEUNEA CERINA (Lehm. & Lindenb.) Schiffn. The species of the tropical genus *Hygrolejeunea* are similar to the Taxilejeuneae and, in some cases at least, form depressed mats. In *H. cerina*, a widely distributed species of Brazil and the West Indies, the pale green, sparingly branched plants grow on the branches of trees and shrubs and may be as much as 5 cm. in length. The stems are about 0.12 mm. in diameter and are similar in structure to those of *Taxilejeunea pterogonia*, except that the medulla is less differentiated and relatively smaller. The cell-walls in cross-sections appear colorless or a pale cream color. The cortical cells (fig. 6, H), seven in number, are mostly 40–60μ in width by 20–30μ in thickness, and their slightly bulging bounding walls are about 4μ thick. The radial walls and the walls between the cortex and medulla equal or slightly exceed the bounding walls in thickness and may be as much as 6μ thick. The medulla is four to six cells across and is composed of cells about 20μ in diameter. The radial walls of the peripheral layer are slightly thickened in the vicinity of the outer tangential walls, but the thickness diminishes rapidly toward the center of the stem, and the inner portions of the radial walls, together with all the walls of the interior medullary cells, are thin.

CYSTOLEJEUNEA LINEATA (Lehm. & Lindenb.) Evans. The genus *Cystolejeunea* is monotypic and its single species, *C. lineata*, is widely distributed in the West Indies, forming pale green depressed mats on trees or growing in admixture with other hepatics. The stems, which give off occasional branches, are about 0.15 mm. in diameter and may attain a length

of 5 cm. or even a little more. Cross-sections show a uniform, pale yellowish brown pigmentation. In its general features the anatomical structure of the stem is much like that of the two preceding species. It shows, in other words, a differentiation into a cortex composed of large cells in seven longitudinal rows and a medulla composed of smaller cells. The cortical cells (fig. 6, I) are 45–60μ wide by 30–40μ thick, and their bounding walls are mostly 8–10μ in thickness. The radial walls and the walls between the cortex and medulla are nearly or quite as thick as the bounding walls. The medullary cells are in five or six layers and average about 19μ in diameter. Except for the outer tangential walls of the peripheral cells, the walls of the medullary cells are thin or only slightly thickened. All the cells, however, show triangular thickenings at the angles, and these may coalesce.

EUOSMOLEJEUNEA TRIFARIA (Nees) Schiffn. The genus *Euomolejeunea* is predominantly tropical, but a few of the species extend into subtropical or temperate regions. Most of the species are yellowish green in color, and many have a more or less pronounced odor. In *E. trifaria*, which is found in most tropical countries throughout the world, the plants form depressed mats on trees. The sparingly branched stems may be 5 cm. or more in length, and the example sectioned was 0.13 mm. wide and 0.11 mm. thick, thus showing a slight dorsiventral compression. The cell-walls in cross-sections are pale yellow throughout. The seven cortical cells (fig. 6, J) are mostly 35–50μ in width by 20–30μ in thickness, and the walls are 8–10μ thick. The outer walls, which bulge more or less, may be bluntly angled, and the periphery of the section in consequence appears crenulate or denticulate. The medulla is about four cells across and its cells average about 20μ in diameter. These cells are all thick-walled, and the walls between the medulla and cortex may be nearly or quite as thick as the walls of the cortical cells; the walls between the medullary cells are a little thinner but show more or less distinct triangular thickenings at the angles. In a few of the walls pits can be demonstrated. Except for the fact that the cell-walls are everywhere thickened, the anatomy of the stem in *Euosmolejeunea trifaria* is much like that of the three preceding Schizostipae.

PYCNOLEJEUNEA MACROLOBA (Mont.) Schiffn. The densely imbricated leaves in *Pycnolejeunea* will serve to distinguish the genus from most of the other Lejeuneae Schizostipae. The species are found in most tropical regions, and a few occur in Chile and Australasia. In the tropical American *P. macroloba* the plants form compact depressed mats on the bark of trees and have a yellowish or yellowish brown color. The stems, which give off a few irregular branches, are mostly 2.5–3.5 cm. in length by 0.09–0.1 mm.

in diameter and appear cream color in cross-sections. Although the cortical cells show the usual arrangement in seven longitudinal rows, most cross-sections have one or two additional cortical cells (fig. 6, K), owing to the crowding together of the leaves and underleaves. The cells in question, which are mostly 25–30μ in width by 20–35μ in thickness, bulge strongly and may even form bluntly angled projections. This is especially true of the two ventral rows. The walls of the cortical cells are about 6μ thick, and pits can be demonstrated in some of the radial walls. The medulla is composed of three or four layers of cells which average about 15μ in diameter. Their walls equal in thickness the walls of the cortical cells, except where pits are present, and these occur not only in the walls between medullary cells but also in the walls between medullary and cortical cells.

LEJEUNEA FLAVA (Swartz) Nees. The generic name *Lejeunea* is here retained for the group of species to which *L. cavifolia* (Ehrh.) Lindb. belongs. It is one of the largest and most widely distributed genera of the Schizostipae, and its range extends to rather high northern and southern latitudes, although the majority of the species are tropical. *L. flava* is perhaps the most widely distributed of all and is found not only in the tropics of both Hemispheres but also in Ireland and the southern United States. The pale green or yellowish green plants are delicate in texture and form depressed mats or thin patches on the bark of trees, on rocks, or even on living leaves. The stems, which branch sparingly and irregularly, show a cream color in cross-sections. They are mostly 1–5 cm. in length by 0.07–0.08 mm. in diameter; and their cortical cells, which show the characteristic arrangement in seven longitudinal rows, measure 25-30μ in width by 15–20μ in thickness (fig. 6, L). The bounding walls of these cells are thin, but the radial walls and the walls between the cortical and medullary cells may be thickened, although their thickness rarely exceeds 6μ. The medulla is mostly four cells across and the cells average about 12μ in diameter. The walls, in some cases, show minute triangular thickenings at the angles of the cells but are otherwise thin throughout.

LEJEUNEA INUNDATA Spruce. The taxonomic position of this aquatic species, which grows on rocks and on branches of trees in the lowlands of Brazil and adjacent regions, is not altogether certain. Spruce placed it in his subgenus *Eu-Lejeunea*, the equivalent of the genus *Lejeunea* as here restricted, but Stephani transferred it to the genus *Potamolejeunea*. The cortical cells of the stem, however, instead of being arranged in numerous longitudinal rows as in *P. orinocensis*, are arranged in only seven longitu-

dinal rows, thus conforming to the usual arrangement found in the Schizostipae. For this reason the species is here retained in *Lejeunea*, although the medulla is more simply organized than in *L. flava*. The medullary cells, in fact, are arranged in only three longitudinal rows. The irregularly branched stems, the cell-walls of which are unpigmented throughout, are mostly 5–7 cm. in length, 0.08–0.1 mm. in width, and a trifle less in thickness. The cortical cells measure 20–30μ in width and thickness and bulge more or less, thus giving the cross-sections a crenulate appearance (fig. 6, M). The outer cell-walls are 3–4μ thick, but the radial and inner tangential walls are thin. The medullary cells average about 25μ in diameter and are thin-walled, except for the more or less pronounced triangular thickenings at the angles.

Simplified types of stem-anatomy, similar to that just described, are to be found in numerous epiphytic Lejeuneae and especially in species that are epiphyllous in habit. Characteristic examples of these will now be considered, and it will be shown that the process of simplification or reduction in certain Paradoxae has progressed even farther than in *L. inundata*.

MICROLEJEUNEA BULLATA (Tayl.) Evans. The genus *Microlejeunea* includes some of the most delicate and inconspicuous of the Lejeuneae. Most of the species are tropical, but a few are found in subtropical or temperate regions. The slender pale green plants of *M. bullata*, which is widely distributed in tropical America as well as in Florida, usually grow scattered on the bark of trees, in many cases mixed with other hepatics. The stems, which branch sparingly, are only 2–3 mm. in length by about 0.03 mm. in diameter. Although seven rows of cortical cells and three rows of medullary cells are present (fig. 6, N) just as in *L. inundata*, the cells are smaller and thin-walled throughout. The cortical cells, for example, are only 6–10μ in width and thickness, and the medullary cells only 4–5μ in diameter. All the cell-walls are unpigmented.

DREPANOLEJEUNEA INCHOATA (Meissn.) Schiffn. The large genus *Drepanolejeunea*, which is predominantly tropical in its distribution, includes both corticolous and epiphyllous species. The neotropic *D. inchoata* belongs to the latter category and grows in irregular pale green patches. The sparingly pinnate stems are mostly 0.5–1 cm. in length by 0.05–0.06 mm. in diameter and agree with the two preceding species in the number and arrangement of the cortical and medullary cells. As seen in cross-section (fig. 6, O) the seven cortical cells are 20–30μ in width by 15–20μ in thickness, and the three medullary cells average about 12μ in diameter. The

unpigmented cell-walls are 2–3μ in thickness, with the exception of the still thinner walls separating the medullary cells from one another.

LEPTOLEJEUNEA ELLIPTICA (Lehm. & Lindenb.) Schiffn. The tropical and subtropical genus *Leptolejeunea* is composed largely, if not entirely, of epiphyllous species, which form irregular pale green patches. The pinnate or bipinnate stems of *L. elliptica*, which is widely distributed in the American tropics, are mostly 0.5–1 cm. long and 0.04 mm. in diameter. The colorless cross-sections (fig. 6, P) are essentially like those of *Microlejeunea bullata*, except that the cells are somewhat larger. The cortical cells, for example, measure 10–15μ in width and thickness, and the medullary cells average about 10μ in diameter.

(*To be concluded*)

A new species of Collybia from Connecticut

Paul W. Graff

(with plate 13)

While recently tramping through an old wood's road in Storrs, Connecticut, my attention was attracted by a young colony of *Collybia* apparently just beginning to produce its first crop of pilei. But four or five young caps were found at that time, though there were very evident indications of a prospective colony of some size. A considerable gray-white mycelial growth was present among decaying woody remains in the soil of the roadway. In view of the apparent possibilities, the locality was revisited the next day, and visits were continued during the subsequent development of the fungus.

This *Collybia* was growing on a corduroy section of an old roadway winding through young mixed, deciduous woods. The young growth is approximately a twenty-five year old stand on the site of an older timbered area. The corduroy material was partly decayed, and to some extent covered with soil in which a few grasses and low weeds were growing. It was evident that the woody substrate was an important factor in the development of the fungus. Though shaded a goodly portion of the day, this section of the road received sunlight for two or three hours during the afternoon. The soil, for some distance about, contained considerable moisture, held by a rich, deep humus. There is a spring and a small swamp in the vicinity which aids in maintaining this moisture supply.

The development of the colony was rapid. The next afternoon eighteen pilei were present, all of which were fully expanded. These were in three clusters, with a few scattered individuals near. Two days later the number of clusters had materially increased, but those previously seen had disappeared, for the most part, leaving only a few decaying remnants. The number of pilei present at this time was much greater, and the clusters larger. In one alone were nine fully matured and closely overlaying caps.

While closely gregarious, in no case was this species found to be truly caespitose, though many members of this genus have that habit. It was also of interest to note that when visited at any time during the afternoon none but fully expanded pilei were found. Hot weather was continuous through the period of these observations. Development from the pilear initials seems to have taken place during the cooler night and early morning hours, to be followed by a brief period of maturity. Early insect attack was the rule, and by mid-afternoon all pilei were thoroughly infested.

On this same day, for some distance from the original colony, scattered individuals were found in the adjacent woods. These appeared in all

cases as solitary pilei. None of the gregarious habit, so pronounced in the material of the road, was to be seen in this habitat. As compared with the other specimens, those of the woods had pilei of relatively lesser diameter. They also had longer and more slender stipes. In color and all other characteristics, however, they appeared identical. The soil of the woods at this place was particularly rich in decaying twigs and branches.

Upon visiting the locality two days later, five days after the plants were first observed, not a single growing individual was to be found, either in the roadway or in the woods. The only clue indicative of the presence of the fungus was one insect infested cap in an advanced state of decay. Subsequent visits to the place during the next two weeks were fruitless. The vigorous rapid development had seemingly been followed by sudden obliteration. Both humidity and temperature were high during this period. The general conditions prevailing were such as to remind one of the difficulties attendant upon the collection and preservation of fleshy fungi in the tropics.

When young the caps of this species open out hemispherically, but soon expand. In doing so they usually become first somewhat umbonate, then irregularly flattened, with sometimes a retention of the central umbo but frequently slightly depressed in the center, due to the raising of the surrounding portion. The margin is frequently irregular as it may be in part slightly repand while other portions are extended or slightly inrolled. This condition is most likely to be found in the clustered forms where some pilei overlap others. In the case of single isolated individuals these irregularities are not so pronounced, and may be absent. The upper surface of the pileus is glabrous and hygrophanous, in texture much like that of *Collybia dryophila* or *C. platyphylla*. It is never sticky when moist as is *C. velutipes*. When fully expanded the cap varies from 7 to 17 cm., in diameter. Among the open road forms the most usual diameter for mature pilei was found to be 13 cm., while 9 cm. was the most usual for the solitary woodland plants.

When fresh the color of the upper surface is, according to Ridgway's "Color Standards," deep colonial buff at a point half way from margin to center, and slightly lighter toward the margin. The center is darker and agrees with Ridgway's avellaneous. Upon drying it was found that these colors fade considerably. Aside from this, there was very little if any variation in color among the large number of individuals observed.

The flesh of the cap is white, and does not change color upon being bruised. It is of a fine soft texture, characteristically thin, and tapers in thickness from its place of union with the stipe toward the margin. The flesh resembles that of *Collybia dryophila* in consistency and form, but not

in variation of color or relative thickness in proportion to the breadth of gills. The thickness of the flesh, midway stipe and margin, is 3 to 6 mm., usually 5 mm., in the heavier road forms and 4 mm., in those of the woodland.

The gills are notably wider than the flesh of the pileus, and, measured at the same locality, vary from 5 to 10 mm. in width. Here again those of the open road vary from those of the woodland, as the former are usually about 8.5 mm. wide and the latter but 6.5 mm. They are white, but may appear faintly cream colored in mature specimens due to the mass of adhering spores. The gills are very crowded, and their edges are somewhat irregular or slightly serrate. Though the gills of most of our common species of *Collybia* are described as adnate or free, in all examples of this species that I have seen they are adnexed. Interspersed among those of full length are shorter free gills, of varying length, and having full rounded ends toward the stipe. All are narrowed and tapering toward the margin.

The stipe is characteristically cylindrical, but with a well rounded bulbous base. The color of it's surface is avellaneous, but of a slightly darker shade than the central portion of the pileus. The interior of the stipe is cartilaginous, stuffed at first, but very soon becoming hollow. The flesh, like that of the cap, does not change color upon being bruised. In the open road forms, whether gregarious or solitary, the stipe varies from 3 to 6 cm. in length, but is usually about 4 cm. in length and 7 mm. thick. As compared with this, the stipe of the woodland form is more slender and longer, usually about 8 cm. in length and 5 mm. in thickness. All forms have a well developed spherical bulb at the base of the stipe. In the open road forms this has a diameter of about 2 cm., while 1.2 cm. is usual for those of the woodland.

The spores are of a very pale creamy tint when mature. Spore prints made upon black paper appear white in color, but when made upon a purely white background this faint creamy tint becomes evident. The average dimension of these spores is $4.2 \times 8.4\mu$. They are not of the ellipsoidal shape most frequently described for members of this genus, but rather are broadly reniform. Upon separation from their sterigmata, the spores are seen to have a short pedicillate appendage of about 1μ in length, by means of which they are attached. The surface of the spores is smooth, and entirely without markings. The basidia are of the typical clavate form, $25\text{–}30 \times 5\text{–}7\mu$, and interspersed among these are frequent cystidia. These cystidia are quite prominent as they extend some 12 to 15μ beyond the basidia. They are sometimes narrowly obovate or fusiform, but typically ventricose, with a dimension of $38\text{–}45 \times 8\text{–}10\mu$. The most striking feature of these cystidia is their prominently stellate apices.

Altogether between fifty and sixty pilei of this species were observed during the several days of their production. Due, however, to very early insect attack and the heaviness of this infestation, no satisfactory effort could be made to test their edibility. Maturity was reached very quickly and disintegration followed rapidly. The odor of the fresh pilei is mild and faintly earthy. There is no special attraction from the mycophagist's viewpoint.

The short, heavy-stemmed, broad-capped forms remind one strongly of the genus *Tricholoma* in their general appearance. That genus, however, is typically one of late summer and autumn. Its stipe is of the same substance as the cap, and its gills are notched or sinuate. In gill character *Tricholoma* is intermediate between *Collybia*, on the one hand, and *Mycena* and *Clytocybe*, on the other.

DIAGNOSIS

Collybia sedula sp. nov.

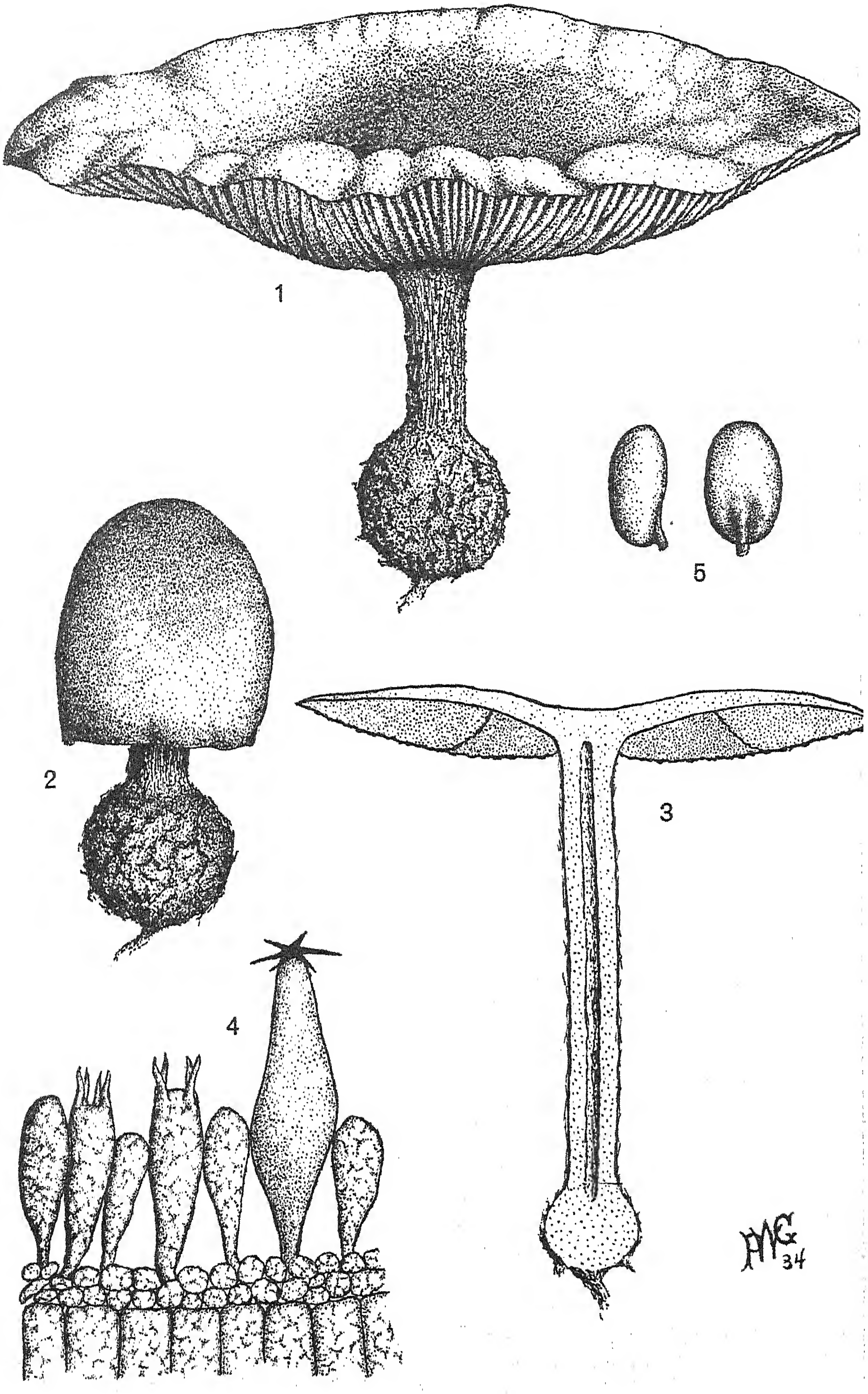
Solitaria vel gregaria; pileo e convexo expanso, primum umbonato, vel omnino expanso, dein convexo-applanato, usque 7–17 cm., (13 cm.) lato; superficie levi, glabra, hygrophana, fulvella, margine pallidiori, centro avellaneo; contextu tenui, albo, 3–6 mm., (5 mm.) lato; lamellis albis, confertis, adnexis, margine sinuati, pluris insertis; stipite recti, cylindrico, arido, fibroso, e farcto cavo, pileo concolor, 3–8 cm., (4 cm.) longis, 0.5–0.7 cm., crassis, basi inflata. 1.2–2.0 cm., diam.; sporis levibus, hyalinis vel pallido-alutaceis, reniformibus, $4.2 \times 8.4\mu$, pedicillatis; basidia clavata, $25–30 \times 5–7\mu$; cystidia fusoidea vel fusoideo-ventricosa, $38–45 \times 8–10\mu$, apice stelliformibus.

Hab. ad terram humosam inter ligna dejecta in silvaticis, Storrs, Tolland County, Connecticut, America Bor., P. W. Graff, 6/21/1934.

Specimens have been deposited in the herbaria of the Connecticut State College, Storrs, Connecticut, and the New York Botanical Garden, Bronx Park, New York City.

Explanation of plate 13

Fig. 1. Young basidiocarp, open road form, natural size.
Fig. 2. Mature basidiocarp, open road form, natural size.
Fig. 3. Section of mature basidiocarp, shaded forest type, natural size.
Fig. 4. Section of hymenium showing basidia and cystidia, $\times 1000$.
Fig. 5. Basidiospores, lateral and inner face as located on the basidium, $\times 2000$.



GRAFF: COLLYBIA SEDULA

The taxonomic and climatic distribution of alkaloids

JAMES B. MCNAIR

In previous papers (McNair 1929–1932) it has been shown that there are relationships between some properties of plant substances and the plants and climates in which they are produced. The study is continued in this article to include vegetable dyes and additional discoveries about alkaloids.

The object of the present study of alkaloids is to bring out the climatic and taxonomic distribution of alkaloids, the relations between the molecular weights, carbon, hydrogen, and oxygen content of alkaloids and the climatic habitats of the plant families producing them; and the specificity of alkaloids as to species, genera, and families.

In another paper (McNair 1931) the relations between the molecular weights, carbon, hydrogen and oxygen content and the climate of habitat were developed with a lesser number (sixty-four) of alkaloids. It is now possible by making use of more of the alkaloids listed by Boas (1927) and the later compilation of Couch (1931) (total 299) to calculate with additional data and probably to arrive at more representative results than those obtained in the earlier article.

CLIMATIC AND TAXONOMIC DISTRIBUTION OF ALKALOIDS

According to the compilation of Boas (1927) and Couch (1931), alkaloids are found in 57 families of gymnosperms and angiosperms. These families are classified climatically by Engler and Gilg (1919), and Willis (1925). An analysis of their data shows that twenty-five, or 43.86%, are mostly tropical; four, or 7.02%, are mostly tropical-subtropical; none is mostly subtropical; three, or 5.26%, are subtropical-temperate; eight, or 14.04%, are temperate; and eighteen, or 31.58%, are widely distributed in habitat.

The climatic distribution of alkaloidal families may be compared with the climatic distribution of the total number of plant families. Making use again of the climatic distribution of these by Engler and Gilg, and Willis, it becomes apparent that of two hundred and ninety-five families of gymnosperms and angiosperms fifty-seven, or 19.32%, contain alkaloids. Of a total number of one hundred and fifty-three tropical families twenty-five, or 16.34%, have alkaloids; of fifteen tropical-subtropical families, four, or 26.6%, have alkaloids; of eight subtropical families none has alkaloids; of seven subtropical-temperate families three, or 63.20%, have alkaloids; of fifty temperate families eight, or 16.00%, have alkaloids, and

fifty-seven families of widely distributed habitats, seventeen, or 29.82%, have alkaloids.

It is evident that of the plant families producing alkaloids three times as many are found in the tropics as in the temperate zone. Those mostly tropical in distribution include 43.86% of all the alkaloid families, while only 14.04% are found growing largely in the temperate zone.

The ratio of tropical alkaloidal families to the total tropical families (16.34%), however, is practically the same as the ratio of temperate alkaloidal families to the total temperate families (16.00%).

The twenty-five tropical alkaloidal families are: Acanthaceae, Aizoaceae, Anonaceae, Apocynaceae, Caricaceae, Cucurbitaceae, Dioscoreaceae, Erythroxylaceae, Hernandiaceae, Lauraceae, Loganiaceae, Loranthaceae, Menispermaceae, Moraceae, Myrtaceae, Palmae, Pedaliaceae, Piperaceae, Rubiaceae, Sapindaceae, Simarubaceae, Stemonaceae, Sterculiaceae, Symplocaceae, and Zygophyllaceae.

The four tropical-subtropical alkaloidal families are: Amaryllidaceae Gnetaceae, Punicaceae, and Theaceae.

No alkaloid-producing family that is largely of subtropical distribution is known.

The three subtropical-temperate distributed alkaloidal families are: Campanulaceae, Nymphaeaceae, and Taxaceae.

The eight alkaloidal families that are mostly temperate in distribution are: Berberidaceae, Cactaceae, Caprifoliaceae, Cruciferae, Papaveraceae, Platanaceae, Ranunculaceae, and Umbelliferae.

The alkaloidal families of widely distributed habitats, of which there are seventeen, are: Aquifoliaceae, Aristolochiaceae, Calycanthaceae, Chenopodiaceae, Compositae, Euphorbiaceae, Fagaceae, Gramineae, Labiatae, Leguminosae, Liliaceae, Malvaceae, Polygalaceae, Rhamnaceae, Rutaceae, Scrophulariaceae, and Solanaceae.

PHYSICAL AND CHEMICAL CONSTANTS IN RELATION TO CLIMATIC DISTRIBUTION

Table 1 brings out certain facts in regard to a probable relationship between climate of habitat and molecular weight, and number of carbon, hydrogen, nitrogen, and oxygen atoms in alkaloids.

Molecular Weights. The maximum and average molecular weights increase markedly from tropical to temperate while the minimum registers a slight decrease.

Carbon Content. The average and minimum number of carbon atoms is the same for both tropical and temperate alkaloids, while the maximum decreases from tropical to temperate.

Hydrogen Content. The minimum and average numbers of hydrogen atoms increase from tropical to temperate, while the maximum numbers indicate a decrease.
Oxygen Content. The maximum, minimum, and average numbers of oxygen atoms increase from tropical to temperate.
Nitrogen Content. Both the average and minimum values for nitrogen are the same in both tropical and temperate families but the maximum decreases from tropical to temperate.

SPECIFICITY OF ALKALOIDS

Of the five families of gymnosperms two, or 40%, have alkaloids. This is a larger proportion than in the angiosperms. Of these, the forty-five families (Willis) of monocotyledons five, or 11.1%, have alkaloids while of the two hundred and forty-one families (Willis) of dicotyledons forty-four, or 18.2%, have alkaloids. The average molecular weights of these are: cryptogams 309, gymnosperms 417, and angiosperms 396.

The alkaloids found in a single plant generally have the closest chemical relationship to each other. Frequently they form a homologous series, often they are isomers, and sometimes stereoisomers. In other instances the difference between these compounds is only in the quantity of hydrogen or oxygen which they possess; accordingly reduction or oxidation will convert one into another. This consideration has led Biddle (1913) to state that, "there seems to be thus an intimate connection between the properties on which the classification of plants is based and those which should naturally determine the classification of alkaloids. The interpretation of such relations will be much simpler, however, when the molecular structure of a much larger number of the plant bases is definitely known."

The alkaloids occurring in any one genus are generally quite closely related: thus the various aconitines have been separated only from members of the genus *Aconitum*, which is noteworthy, in giving a new chemical species of aconitine for each new botanical species analyzed, though all the aconitines are apparently closely related. An idea of the value of alkaloids (chemical characters) as complements of morphological characters in taxonomy may be gained by the study of two papers dealing with the revision of the genus *Cinchona*, viz., that of Rusby (1932) versus Standley (1931).

The same alkaloid is seldom found in different plant families, but on the contrary an alkaloid is often characteristic of one family, e.g., protopine occurs in many plants of the Papaveraceae and is not found in other families.

Where different alkaloids are met with in the same family each is generally confined to a single genus, and a better classification of these alkaloids is therefore obtained by dividing the family according to genera. In large families the alkaloids of the different genera are usually in close agreement when grouped according to tribes. For instance:

Papaveraceae

Subfamily II. Paperoideae:

Tribe 1, Eschscholtzieae: (ionidine, $C_{11}H_{25}O_4N_4$) *Eschscholtzia*

Tribe 2, Chelidoneae: (methoxychelidonine, $C_{21}H_{21}O_6N$) *Chelidonium*

Tribe 3, Papaveraceae: (glaucine, $C_{21}H_{25}O_4N$) *Glaucium*, (codamine, $C_{21}H_{25}O_4N$) (tritopine, $C_{42}H_{54}O_7N_2$) (lanthopine, $C_{23}H_{25}O_4N$) (narcotine, $C_{22}H_{23}O_7N$) (laudanosine, $C_{21}H_{27}O_4N$) (cryptopine, $C_{21}H_{23}O_5N$) (laudanine, $C_{20}H_{25}O_4N$) (papaverine, $C_{20}H_{21}O_4N$) (protopine, $C_{20}H_{19}O_5N$) (pseudomorphine, $C_{17}H_{18}O_3N$) (morphine, $C_{17}H_{19}O_3N$) (codeine, $C_{18}H_{21}O_3N$) (isothebaine, $C_{19}H_{21}O_3N$) (thebaine, $C_{19}H_{21}O_3N$), *Papaver*

Subfamily III. Fumarioideae:

(dicentrine, $C_{20}H_{21}O_4N$) *Dicentra*, (corycavine, $C_{23}H_{23}O_6N$) (corydaline, $C_{22}H_{27}O_7N$) (dehydrocorydaline, $C_{22}H_{25}O_5N$) (corycavidine, $C_{22}H_{25}O_5N$) (corybulbine, $C_{21}H_{25}O_4N$) (isocorybulbine, $C_{21}H_{25}O_4N$) (corycavanine, $C_{21}H_{21}O_5N$) (isocordine, $C_{20}H_{23}O_4N$) (corydine, $C_{20}H_{23}O_4N$) (corytuberine, $C_{19}H_{21}O_4N$) (bulbocapinine, $C_{19}H_{19}O_4N$) *Corydalis*

Solanaceae

Tribe 2, Solaneae: (atropine, $C_{17}H_{23}O_3N$) (tropine, $C_8H_{15}ON$) (belladonine, $C_{17}H_{21}O_2N$) *Atropa*, (hyoscyamine, $C_{17}H_{23}O_3N$) (tropine, $C_8H_{15}ON$) (nor-hyoscyamine, $C_{16}H_{21}O_2N$) (hyoscine, $C_{17}H_{21}O_4N$) *Hyoscyamus*, (solanidine, $(C_{18}H_{31}ON)_2$) (solanine, $C_{54}H_{92}O_{18}N_2$) *Solanum*

Tribe 4, Cestreae: (nicotine, $C_{10}H_{14}N_2$) (nicoteine, $C_{10}H_{12}N_2$) (nicotelline, $C_{10}H_8N_2$) *Nicotiana*

Leguminosae

Subfamily I. Mimosoideae:

Tribe 6, Parkieae: (paucine, $C_{27}H_{39}O_5N_5$) *Pentaclethra*

Subfamily III. Papilionatae:

Tribe 1, Sophoreae: (ormosine, $C_{20}H_{33}N_3$) *Ormosia*, (matrine, $C_{15}H_{24}ON_2$) *Sophora*

Tribe 2, Podalyrieae: (lupanine, $C_{15}H_{24}ON_2$) (lupinine, $C_{21}H_{40}O_2N_2$) (lupinidine, $C_{15}H_{26}N_2$) (spathulatine, $C_{33}H_{64}O_5N_4$) *Lupinus*, (spar-

teine, $C_{15}H_{26}N_2$) *Spartium*, (retamine, $C_{15}H_{26}ON_2$) *Retama*, (sarothamnine, $C_{15}H_{24}N_2$) (genistaine, $C_{16}H_{28}N_2$) *Sarothamnus*

Tribe 5, Loteae: (galegine, $C_6H_{13}N_3$) *Galega*

Tribe 7, Hedysareae: (arachine, $C_5H_{14}ON_2$) *Arachis*

Tribe 10, Phaseoleae: (hyaphorine, $C_{14}H_{18}O_2N_2$) *Erythrina*, (physovenine, $C_{15}H_{12}O_3N_8$) (eseramine, $C_{16}H_{25}O_3N_4$) (eserine, $C_{15}H_{21}O_2N_3$) (isophysostigmine, $C_{15}H_{21}O_2N_3$) (geneserine, $C_{15}H_{21}O_3N_3$) (eseridine, $C_{15}H_{23}O_3N_3$) *Physostigma*

Rubiaceae

Subfamily I. Cinchonoideae:

Tribe 3, Rondeletieae: (aribine, $C_{23}H_{20}N_4$) *Arariba*

Tribe 5, Cinchoneae: (cinchonidine, $C_{19}H_{22}ON_2$) (cinchonine, $C_{19}H_{22}ON_2$) (cinchotine, $C_{19}H_{24}ON_2$) (quinine, $C_{20}H_{24}O_2N_2$) (quinidine, $C_{20}H_{24}O_2N_2$) *Cinchona*, (cinchonine, $C_{19}H_{22}ON_2$) (quinine, $C_{20}H_{24}O_2N_2$) (cinchotine, $C_{19}H_{24}ON_2$) (concusconine, $C_{23}H_{26}O_4N_2$) (chairamine, $C_{22}H_{26}O_4N_2$) (conchinamine, $C_{19}H_{24}O_2N_2$) (chinamine, $C_{19}H_{24}O_2N_2$) (cupreine, $C_{19}H_{22}O_2N_2$) (diconchinine, $C_{40}H_{46}O_3N_4$) (homochinine, $C_{39}H_{46}O_4N_4$) (conchairamidine, $C_{22}H_{26}O_4N_2$) *Remijia*, (hymenodictine, $C_{23}H_{40}N_2$) *Hymenodictyon*, (corynantheine, $C_{22}H_{28}O_4N_2$) (hydroyohimbine, $C_{21}H_{28}O_3N_2$) (mesoyohimbine, $C_{21}H_{26}O_3N_2$) (isoyohimbine, $C_{21}H_{26}O_3N_2$) *Corynanthe*

Tribe 6, Naucleeae: (mitraversine, $C_{22}H_{26}O_4N_2$) (mitragyrine, $C_{22}H_{31}O_5N$) *Mitragna*, (rhynchophylline, $C_{22}H_{28}O_4N_2$) *Ourouparia*

Tribe 15, Psychotrieae: (cephaeline, $C_{28}H_{38}O_4N_2$) (psychotrine, $C_{28}H_{36}O_4N_2$) (emetine, $C_{30}H_{40}O_4N_2$) *Cephaelia*

A small number of alkaloids occur in various plants which possess no close botanical relationships to each other. Some of these seem to have no particular physiological activity. The purine alkaloids caffeine and theobromine supply an instance of closely related alkaloids occurring in plants belonging to widely different (tropical) families. Some alkaloids are found in the same orders, e.g., bebeerine and laurotetanine are both found in the Ranales. Other alkaloids each of which is found in two or more families are: (tropical) brucine (molecular weight 394), bebeerine (297), laurotetanine (327), and yohimbine (368); (temperate) (canadine (339), chelidonine (353), chelerythrine (347), homochelidonine (369), and narceine (445), and (widely distributed) allantoine (158), bebeerine (353), choline (121), cytisine (190), hordeine (165), sanquinarine (333), stachydrine (143), and trigonelline (137).

It has been suggested by Pictet and Biddle (1913) that some of these, namely, the members of the purine, choline, and asparagine groups, differ

from the more specific alkaloids in appearing not to be *assimilation products* of the plant organism, but *decomposition products* of more complicated derivatives.

In support of the Pictet and Biddle suggestion, it is evident that in the animal metabolism purine bodies, such as uric acid, which appear in the urine are decomposition products from compounds of larger molecular weights. Choline, widely distributed in the animal and vegetable kingdoms, is a decomposition product of lecithine, is contained in hops, and also in the alkaloid sinapine, which occurs in mustard seeds; it is produced in corpses, as the result of putrefactive changes.

It is interesting to note that the average molecular weights, of the alkaloids which are found in more than one plant family, are lower than the average molecular weights of the other alkaloids which are confined to individual families in the same climate of habitat. A similar statement applies to the alkaloids of maximum molecular weight.

These low molecular weights of alkaloids of wide botanical distribution certainly indicate that the more simple alkaloids are more widely distributed than the more complex. These simpler alkaloids may perhaps be either the decomposition products of more complex substances or the nuclei (building stones) of more complex compounds.

SUMMARY

Alkaloids are found in fifty-seven families of gymnosperms and angiosperms; of these 44% are mostly tropical and 14% are temperate.

The ratio of tropical alkaloidal families to the total tropical families (16.34%) is practically the same as the ratio of temperate alkaloidal families to the total temperate families (16.0%).

The maximum and average molecular weights increase markedly from tropical to temperate, while the minimum registers a slight decrease.

The average and minimum number of carbon atoms is the same for both tropical and temperate alkaloids while the maximum decrease from tropical to temperate.

The minimum and average numbers of hydrogen atoms increase from tropical to temperate while the maximum numbers indicate a decrease.

The maximum, minimum, and average numbers of oxygen atoms increase from tropical to temperate.

Both the average and minimum values for nitrogen are the same in both tropic and temperate families but the maximum decreases from tropical to temperate.

Alkaloids are found in 40% of the gymnosperm families, 11% of the

TABLE 1

Variations in the composition of alkaloids in relation to climate of habitat

HABITAT	MOLECULAR WEIGHT			CARBON			HYDROGEN			OXYGEN			NITROGEN		
	MAX.	MIN.	AVER.	MAX.	MIN.	AVER.	MAX.	MIN.	AVER.	MAX.	MIN.	AVER.	MAX.	MIN.	AVER.
Tropical	634	121	333	36	8	17	55	11	22	6	0	2	4	1	1
Tropical-subtropical	572	135	243	18	5	10	21	5	14	5	1	2	4	1	2
Subtropical	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Subtropical-temperate	669	285	376	37	18	25	51	25	40	10	2	5	2	1	1
Temperate	698	125	379	29	8	17	39	17	24	11	0	5	2	1	1
Widely distributed	1057	118	320	32	7	17	41	13	21	13	0	4	3	1	2

monocotyledons, and 18% of the dicotyledons. The molecular weights are larger in the angiosperms than in the gymnosperms.

Alkaloids in the same plant generally bear the closest chemical relation to one another.

Alkaloids found in any one genus are usually somewhat closely related.

The same alkaloid is rarely met with in different plant families.

Where different alkaloids are met with in the same family they are generally each confined to a single genus.

In large families the alkaloids of the different genera are usually in close agreement when grouped according to tribes.

A small number of these compounds are found in more than one family.

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Additional notes on tautonyms

Harold N. Moldenke

In April, 1932, I published an article entitled "A discussion of tautonyms"[1] in which 228 of these bizarre binomials were listed, together with what I considered to be the oldest valid non-tautonymous name within the given genus for the plant in question in each case. In March, 1934, in an article entitled "A supplementary list of tautonyms and miscellaneous nomenclatural notes"[2] thirteen more such tautonyms were listed.

Since these two papers went to press, a number of inaccuracies in the first of them have been called to my attention. Among these are eight cases where the given tautonymous combination was validly published previous to the citation given by myself in my original list. Although in almost every case one will find, if one looks up the reference cited by myself, that the tautonymous combination is actually proposed there as a new one, yet these proposals appear upon further investigation to have been made in ignorance of the fact that the proposed binomials had already been published previous to that date. The following, then, are the correct citations for these eight tautonyms:

Cedrus Cedrus (L.) Huth, Helios **11**: 133. 1893.
Cydonia Cydonia (L.) Pers. Syn. Pl. **2**: 40. 1807.
Damasonium Damasonium (L.) Aschers. & Graebn. Syn. Mitteleur. Fl. **1**: 389. 1898.
Lycopersicon Lycopersicon (L.) Karst. ex Lyons, Pl. Names 232. 1900.
Malus Malus (L.) Britton in Britton & Br. Ill. Fl., ed. 1, **2**: 236. 1897.
Vaccaria Vaccaria (L.) Huth, Helios **11**: 136. 1893.
Vanilla Vanilla (L.) Huth, Helios **11**: 136. 1893.
Vitis-Idaea Vitis-Idaea (L.) Britton, Man. 708. 1901.

In addition to the binomials mentioned above, the following have also been proposed as new more than once, and the citations given below will often be found quoted as the correct ones for the binomials in question. In each of the following cases, however, the combination is antedated by the reference cited by me in my original list. The references below are given here merely as a matter of record.

Abies Abies (L.) Druce, Rep. Bot. Exch. Cl. Brit. Isles **7**: 689. 1925.
Abutilon Abutilon (L.) Rusby, Mem. Torrey Club **5**: 222. 1894.
Adhatoda Adhatoda (L.) Lyons, Pl. Names 15. 1900.
Alliaria Alliaria (L.) Britton, Mem. Torrey Club **5**: 167. 1894.
Ananas Ananas (L.) Lyons, Pl. Names 32. 1900.

[1] Bull. Torrey Club **59**: 139–156.
[2] Torreya **34**: 5–10.

Arisarum Arisarum (L.) Dörfler, Herb. Norm. No. 3270. 1897.
Castanea Castanea (L.) Sudworth, Bull. Torrey Club **19:** 152. 1892.
Castanea Castanea (L.) Lyons, Pl. Names 85. 1900.
Cedrus Cedrus (L.) Lyons, Pl. Names 88. 1900.
Cetarach Cetarach (L.) Lyons, Pl. Names 92. 1900.
Colocasia Colocasia (L.) Lyons, Pl. Names 111. 1900.
Corallorhiza Corallorhiza (L.) MacM., Bull. Torrey Club **19:** 15. 1892.
Cotinus Cotinus (L.) Karst. ex Lyons, Pl. Names 119. 1900.
Cubeba Cubeba (L. f.) Lyons, Pl. Names 124. 1900.
Cydonia Cydonia (L.) Lyons, Pl. Names 127. 1900.
Dracunculus Dracunculus (L.) Druce, Brit. Pl. List, ed. 2, 115. 1928.
Eragrostis Eragrostis (L.) MacM. Metasp. Minn. 75. 1892.
Eragrostis Eragrostis (L.) Karst. Deutsch. Fl. 389. 1881.
Filipendula Filipendula (L.) Aschers. & Graebn. Syn. Mitteleur. Fl. **6**^{1}**:** 439. 1902.
Lagenaria Lagenaria (L.) Lyons, Pl. Names 213. 1900.
Lens Lens (L.) Lyons, Pl. Names 219. 1900.
Leontopodium Leontopodium (L.) Lyons, Pl. Names 219. 1900.
Levisticum Levisticum (L.) Lyons, Pl. Names 223. 1900.
Limonium Limonium (L.) Druce, Rep. Bot. Exch. Cl. Brit. Isles **7:** 583 & 687. 1925.
Malvaviscus Malvaviscus (L.) Millsp., Field Columb. Mus. Pub. Bot. **2:** 73. 1900.
Manihot Manihot (L.) Lyons, Pl. Names 239. 1900.
Moringa Moringa (L.) Small, Fl. SE. U.S. 491. 1903.
Nelumbo Nelumbo (L.) MacM. Metasp. Minn. 226. 1892.
Omphalodes Omphalodes (L.) Druce, Rep. Bot. Exch. Cl. Brit. Isles **7:** 688. 1925.
Opopanax Opopanax (L.) Lyons, Pl. Names 266. 1900.
Opuntia Opuntia (L.) Coult., Contr. U.S. Nat. Herb. **3:** 432. 1896.
Petroselinum Petroselinum (L.) Lyons, Pl. Names 282. 1900.
Phragmites Phragmites (L.) MacM. Metasp. Minn. 73. 1892.
Pimenta Pimenta (L.) Lyons, Pl. Names 290. 1900.
Pyracantha Pyracantha (L.) Aschers. & Graebn. Syn. Mitteleur. Fl. **6**^{2}**:** 11. 1906.
Taraxacum Taraxacum (L.) MacM., Bull. Torrey Club **19:** 15. 1892.
Thevetia Thevetia (L.) Lyons, Pl. Names 370. 1900.
Ugni Ugni (Mol.) Macloskie, Rep. Princeton Univ. Exped. Patag. **8:** 602. 1905.
Viscaria Viscaria (L.) Degen., Magyar Bot. Lap. **4:** 122. 1905.
Zingiber Zingiber (L.) Rusby ex Lyons, Pl. Names 402. 1900.

It is also worth noting that a rather serious orthographic error occurs on page 147 of my first list, where the name "LEPTOSTACHYS LEPTOSTACHYS" is recorded and accredited to MacMillan. *Leptostachys* is a generic name proposed by G. F. W. Meyer in the *Gramineae* and by Ehrhart in the *Cyperaceae*. In neither case has the above-mentioned tautonymous combination been proposed. The binomial which MacMillan proposed and to which I referred in my list was *Leptostachya Leptostachya*, a synonym of *Phryma Leptostachya* L. [*Leptostachya carolinensis* Kuntze] in the *Phrymaceae*.

As a matter of record, it should also be noted that the orthographic variant "*Ecastaphyllum Ecastaphyllum*" appears in the Index Kewensis, although in the reference there cited one finds that the binomial as originally proposed by Huth was written *Ecastophyllum Ecastophyllum*.

The following additional tautonyms, never before listed by myself, have come to light since the publication of my second article on this subject:

CALCITRAPA CALCITRAPA Hill, Hort. Kew. 62. 1768.
=*Calcitrapa stellaris* Hill, Herb. Brit. 1: 76. 1769.
CROCODYLIUM CROCODYLIUM (L.) Hill, Hort. Kew. 63. 1768.
=*Crocodilium syriacum* Cass., Dict. Sci. Nat. 12: 19. 1818.
ERIOPHA ERIOPHA Hill, Hort. Kew. 69. 1768.[3]
=*Centaurea eriophora* L. Sp. Pl. 916. 1753.
RHAPONTICA RHAPONTICA (L.) Hill, Hort. Kew. 69. 1768.
=*Rhaponticum scariosum* Lam. Fl. Fr. 2: 38. 1778.

On page 147 of his "Hortus Kewensis" Hill lists under the generic name *Mandragora* one species, as follows: "1. *Mandragora. Atropa Mandragora.*" On page 148 he cites under the generic name *Battata* one species in the same manner: "1. *Battata. Solanum Tuberosum.*" The Index Kewensis considers the latter as valid publication of "*Battata tuberosa* Hill." If this is so, then the former is certainly valid publication of "*Mandragora Mandragora* Hill," a combination not listed in the Index Kewensis. The inconsistency of the Index Kewensis in its policy toward this work of Hill is well illustrated by the following additional example. On page 148, under the genus *Lycopersicum*, Hill again cites only one species, as follows: "1. *Lycopersicum. Solanum Lycopersicum.*" This the Index Kewensis lists as "*Lycopersicum Solanum-Lycopersicum* Hill"!

In several instances the non-tautonymous names which I gave as the correct ones in that particular genus in my original list have been found to

[3] Hill implies that this is a new combination for "*Centaurea Eriopha*," but no such name was ever published as far as I have been able to ascertain. The species referred to was undoubtedly Linnaeus' *Centaurea eriophora*. The genus *Eriopha* is not maintained by anyone today and no other binomials have even been published in it.

be antedated by other binomials. For the sake of accuracy I am listing these tautonyms again below, together with the non-tautonymous binomials which further investigations have revealed to be the correct ones in each instance:

ANANAS ANANAS (L.) Voss, Vilmorin's Blumeng., ed. 3, **1**: 964. 1895.
 = *Ananas comosus* (L.) Merr. Interpret. Rumph. Herb. Amb. 133. 1917.
HELENIUM HELENIUM (Nutt.) Small, Fl. SE. U.S. 1292 & 1341. 1903.
 = *Helenium decurrens* (Macbride) Moldenke.[4]
OXYCOCCUS OXYCOCCUS (L.) MacM., Bull. Torrey Club **19**: 15. 1892.
 = *Oxycoccus quadripetalus* Gilib. Fl. Lithuan. **1**: 5. 1781.
PERSEA PERSEA (L.) Cockerell, Bull. Torrey Club **19**: 95. 1892.
 = *Persea americana* Mill. Gard. Dict., ed. 8. 1768.
POROPHYLLUM POROPHYLLUM (L.) Kuntze, Rev. Gen. Pl. 3^2: 168. 1898.
 = *Porophyllum ruderale* (Jacq.) Cass., Dict. Sci. Nat. **43**: 56. 1826.

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[4] **Helenium decurrens** (Macbride) Moldenke, comb. nov. *Leptopoda decurrens* Macbride ex Ell. Bot. S. C. & Ga. **2**: 446. 1824. This is the plant originally called *Leptopoda Helenium* Nutt. [Gen. **2**: 174. 1818] and then *Leptopoda helenioides* Cass. [Dict. Hist. Nat. **26**: 80. 1823]. The combination *Helenium Helenium* (Nutt.) Small cannot be used because it is a tautonym, and the use of *Helenium helenioides* is precluded by the *Helenium helenioides* of Clements & Clements [Rocky Mt. Fl. 279. 1914], an entirely different species of the Rocky Mountains.

INDEX TO AMERICAN BOTANICAL LITERATURE
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The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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A developmental analysis of size and shape in tomato fruits

Helen B. Houghtaling

(with plate 14)

To understand the way in which genes produce their effects it is of the utmost importance to find the visible changes which take place as a genetically controlled character develops. It has been the chief object of workers in the past to show that characters are inherited and to determine the chromosome mechanism involved. This work has been limited to the study of mature characters and the developmental aspect of the problem has largely been ignored. The object of the present study was to determine how differences in shape and size arise during development in the fruits of various genetically distinct types of *Lycopersicum esculentum* and in *L. pimpinellifolium*.

The work of Hedrick and Booth (1907), Price and Drinkard (1908), Groth (1915), Warren (1924), Lindstrom (1926-1932) and MacArthur (1925-1931) indicates a genetical basis for the inheritance of size and of shape in tomato fruits. Elongate shape is shown to be a single Mendelian recessive to spherical shape and has been located definitely in chromosome I. Size factors, although they have not been shown to give simple Mendelian ratios, have been found to be linked with specific characters such as fruit shape, color of epidermis, stem color and color of pericarp. Therefore, we may assume that the shapes and sizes which are to be studied in this paper are the results of gene activity.

MATERIALS AND METHODS

Seven varieties of *Lycopersicum esculentum* (table 1) differing as widely as possible in fruit size and shape, and the currant tomato, *L. pimpinellifolium*, were grown in the greenhouse during the winter of 1932. A number of hybrids were secured between the various types.

The hybrids and inbred lines from the original varieties were grown in the field during the summer of 1933. Material from these plants was fixed in 70% alcohol containing 6% formalin. Flowers were collected and fixed on the day of flowering. Stages before flowering and also developing fruits were fixed separately. Full-sized green fruits were collected early in September. These were weighed and then cut along the polar diameter and outlined on paper for a record of their shape and size. The number of car-

[The Bulletin for April (62: 177–242) was issued April 1, 1935]

pels was counted and a comparable portion of the pericarp of each fruit fixed. Volume of fruit and ovary was calculated from the dimensions by squaring the width (equatorial diameter), and multiplying it by the length, (polar diameter). This is thought to give a better measure of size than weight, since the specific gravity of the fruit changes rapidly as it ripens and is different in large and small fruited types (Lindstrom, 1926). More-

TABLE I

	FRUIT SIZE, CC.	SHAPE INDEX	NUMBER OF CARPELS	PERICARPING CELL SIZE MATURITY $\times 10^{-7}$ cc.	OVARY SIZE FLOWERING $\times 10^{-4}$ cc.	OVARY SHAPE AT INDEX FLOWERING	CELL SIZE AT FLOWERING $\times 10^{-10}$ cc.
Red Cherry	10.4	1.06W	2.00	78.7	16.6	1.27L	68.6
Red Plum	29.2	1.28L	2.00	150.0	22.9	1.87L	74.0
Red Pear	24.4	1.66L	2.00	91.7	29.2	2.25L	68.8
Yellow Pear	31.0	1.64L	2.00	173.0	20.7	2.61L	62.0
Red Peach	74.1	1.18W	2.60	138.0	45.0	1.08L	71.8
Yellow Peach	75.4	1.22W	3.20	225.0	31.4	1.22L	73.7
Bonnie Best	275.0	1.48W	4.25	268.0	161.7	1.53W	75.4
Red Currant	1.54	1.01W	2.00	18.4	5.1	1.27L	82.0
Plum×Cherry	15.0	1.01W	2.00	109.0	20.7	1.58L	79.8
Cherry×Y. Peach	19.7	1.14W	2.50	71.3	35.2	1.23L	73.9
R. Peach×Cherry	22.9	1.17W	3.20	96.0	13.3	1.23L	81.5
Frogmore×Cherry	44.1	1.22W	2.54	285.0	22.5	1.19L	83.2
R. Pear×Y. Peach	43.6	1.01L	3.24	139.0	28.4	1.37L	84.9
R. Cherry×R. Pear	14.9	1.03L	2.22	115.0	19.7	1.59L	74.0
Cherry×Bonnie Best	38.9	1.19W	3.16	153.0	50.2	1.02L	82.0
Bonnie Best×Cherry	41.8	1.23W	3.07	207.0	39.4	1.24L	86.5
R. Pear×Bonnie Best	72.0	1.05L	3.42	202.0	42.1	1.37L	78.8
Bonnie Best×Y. Pear	75.9	1.09L	3.71	395.0	22.8	1.52L	68.3
R. Pear×R. Plum	60.7	1.11L	3.60	196.0	24.3	1.33L	73.5
R. Pear×R. Peach	46.3	1.00	3.30	197.0	20.8	1.49L	78.7
Red Plum×R. Currant	4.2	1.03W	2.00	67.8	6.7	1.38L	82.2
Red Cherry×R. Currant	2.6	1.09W	2.00	34.6	5.0	1.15L	75.6

over, it was impracticable to get weight on very early stages of development and a value for fruit size was wanted which might be directly compared with values for the very early stages.

The material was imbedded in paraffin and sectioned, early stages 10 microns thick, later stages 15 and 20 microns thick. The early stages were projected at a magnification of 45x and 125x and measured from these projections. Later stages approaching one centimeter in diameter were measured directly. The values for mature fruits were taken from the outlines which had been drawn of them.

Cell size was measured in the ovary wall (later the pericarp). Transverse and longitudinal microtome sections showed the cells to be essen-

tially spherical except for very early stages when they were somewhat elongated along the polar axis. In measuring cells longitudinal sections were used throughout. The cells were projected at magnifications of 125x and 200x except for stages at flowering and before flowering, when the cells are so densely filled with protoplasm that the use of the projector was impracticable. Measurements on these early stages were made by a micrometer eye piece. The cells which were projected were drawn, a single field being chosen from the middle region of the pericarp in developing fruits, and two adjoining fields in the mature ones. The longest diameter and the diameter at right angles to this were measured on the ten largest cells. These were averaged and volume was computed (by employing the formula for the volume of a sphere). The geometric mean of the ten cells was computed and taken as the cell size in the individual fruits.

Measurements from five flowers (or fruits) were determined and were averaged to obtain the values for ovary (and fruit) size and for cell size.

All averages in table 1 are geometric. This is believed to give a truer value of the mean than an arithmetic average since all measurements are on growing tissues. The geometric mean was calculated by averaging the logarithms of the various values studied and finding the antilog of the average logarithm. The correlation tables and all charts are plotted on logarithmic scales. Standard errors of correlation coefficients are given.

DEVELOPMENT OF FRUIT

Cooper (1927) describes the development of the tomato flower using the varieties Bonnie Best and Greater Baltimore. Flowers are formed in a racemose cyme and several developmental stages may be found in a cluster so that it is not difficult to trace stages. From a more or less flat meristem sepal primordia arise, then petals and stamens and ovary primordia with a spiral order of origin. The ovary primordia elongate; the upper portion forms the stigma and style and the base thickens, forming the ovary. A placenta is formed, with developing ovules. Shortly after flowering the style falls off and the petals and stamens wither. The calyx enlarges and remains attached to the base of the developing fruit. The ovary continues to grow and develops into the mature fruit. Shortly after fertilization the placental tissue grows up around the ovules and the cells become very large, ultimately rupturing as the fruit becomes ripe.

DEVELOPMENT OF SHAPE

Shape differences may arise developmentally in a number of ways. Sinnott and Kaiser (1933) found that the difference in shape of two types of pepper (*Capsicum annuum*) is the result of different relative rates of

growth of length and width in developmental stages after flowering. In squash (*Cucurbita Pepo*) however, they found that the mature shape is not the result of such a differential growth rate, since it is already established in the early ovary primordium, and growth in the various dimensions proceeds at approximately the same rate.

The shape of the varieties of tomatoes studied here varies from the elongate pear type with length 1.65 times width to the flattened Bonnie Best whose width is 1.48 times its length. The hybrids vary in their relationship to the parent types but the general tendency is toward a spherical form.

In studying development of shape Huxley's formula (1932) $y = bx^k$ was employed. For shape, length (y) was plotted against width (x) logarithmically. The slope of the resulting line (or the value of k) measures the relative rate of growth of length and width.

Between flowering and maturity ovary length grows slightly more slowly than width, ($k = 0.9$), but the relative growth of dimensions in all types after flowering is approximately equal, as it is in squash throughout development, so that shape is essentially determined by flowering. The correlation between shape at flowering and shape at maturity is $+.9198 \pm .0013$. The shape differentiation of the ovary thus takes place between the stage of the earliest flat primordium and the ovary of the flower. The ovary primordium of the pear grows rapidly in length at first with only slight increase in width ($k = 1.80$) so that the elongate shape is established very early in development. The sphere forms also grow most rapidly in length in the early stages ($k = 1.30$), and in the flattened types length grows only slightly faster than width ($k = 1.03$). This is in marked contrast with the development of shape in peppers where types remain essentially the same up to flowering and differentiation occurs afterwards. In tomatoes the genes for shape act at a very early period and apparently operate by determining the relative polarity of cell division, since there is no marked difference in cell shape or size at this critical stage.

RELATIONSHIP OF SIZE AND SHAPE

Sinnott (1935) found no necessary relationship between size and shape in the second generation of crosses between large and small fruited squash and has presented evidence that the two aspects of development are quite independent of each other. Lindstrom (1929) found a relationship in tomatoes but concluded that it is caused by linkage between certain size and shape genes rather than by the mechanism through which shape is determined. In tomatoes shape is chiefly differentiated early in development but during later growth there is a slight added divergence since width in-

creases a little faster than length. Therefore in a pure line or F_1 a slight positive correlation between size and increased flattening might be expected. There is no significant correlation, however ($+.1776 \pm .1411$), between size and shape index in the tomato types studied here. Another factor enters the problem in that highly fasciated (multicarpellate) types tend to be both flatter and also larger than bicarpellate types. If *L. pimpinellifolium* and its hybrids, all of which are bicarpellate, are excluded the correlation between size and shape is higher ($.3402 \pm .0973$). The relationship between size and number of carpels is $+.7655 \pm .0115$ and between shape and the

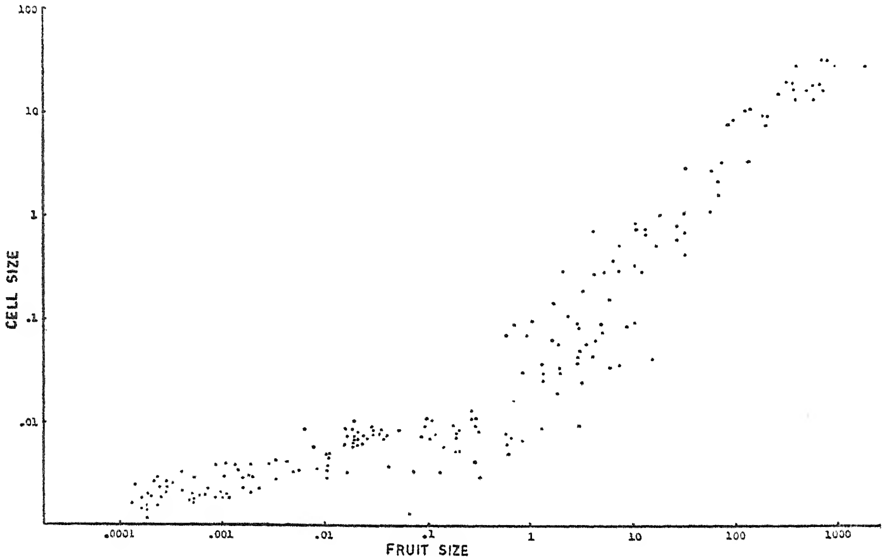

Fig. 1. Cell size plotted against fruit (and ovary) size, both logarithmically, throughout fruit development in all types of *Lycopersicum esculentum*. Fruit size in units of 10 cc.; cell size in units of 10^{-6} cc.

number of carpels is $+.4202 \pm .0701$. This latter relationship seems to be a mechanical one, for the fasciated types start from a broader meristematic platform than the others and the length of the ovary primordia would have to grow at a much greater rate with respect to width than has been observed in any of the fruit types to produce an elongate fasciated type within the period when shape is determined.

DEVELOPMENT OF SIZE

The size of the individual organ is associated with the original amount of growing tissue, the rate at which it grows and the point at which it stops growing. Sinnott (1921), Reed (1927) and Ashby (1932) conclude that ultimate size is determined largely by original size.

In the tomatoes here studied differences in fruit size are well established by the time of flowering (plate 14, figures 7 to 11) for the coefficient of correlation between ovary size at flowering and mature fruit size is $+.8789 \pm .0031$. Indeed, marked differences are evident at a much earlier stage, when the ovary primordium is just beginning its development, as is shown in figures 1 to 6. The size differences thus established early are maintained throughout development.

The problem arises as to whether these differences, which reach their culmination in the mature fruit, are associated with differences in number of cells, in size of cells, or in both these respects. In studying this problem in developing tomatoes the size (volume) of cells in the mid-region of the ovary wall was plotted against ovary (and fruit) size logarithmically. In the formula, $y = bx^k$, y is cell size and x is fruit size. Text figure 1 shows the result for all the *L. esculentum* pure lines and hybrids combined. In general there is but slight increase in cell size with enlarging ovary size until just before flowering, but shortly after that the increase is marked and directly proportional to increase in fruit size ($k = 1$). This is interpreted to mean that the cells remain small and actively meristematic until some period near flowering, when cell division ceases rather abruptly, and that all further growth is due entirely to increase in cell size.

Figure 2 shows the curves which fit the points for the different pure types of *L. esculentum*. *L. pimpinellifolium* is shown by a broken line. Unlike *L. esculentum*, in this species some cell division must persist through the entire course of development since fruit size is constantly increasing faster than cell size, k being only .74. Line 2 represents the variety Red Cherry, 3 the Pear, 4 the Plum, 5 Peach and 6 Bonnie Best. In Red Cherry cell division ceases relatively early in ovary development and cell enlargement stops when the cells are relatively small. In the Pear, cell division continues progressively further and cell size reaches a progressively higher value; and in the largest fruit, Bonnie Best, cell division persists the longest and cell size reaches its highest value.

The Cherry-Currant and Plum-Currant hybrids give curves intermediate between their parents. Cell division continues longer than in the esculentum types but not as long as in the pimpinellifolium. In general the curves of the esculentum crosses are intermediate between their parents. It is noteworthy that the shape of the developmental curve is essentially similar in all the varieties of *L. esculentum* though the abruptness of the change increases in the larger types. The length of the period during which cell division occurs (and thus the number of cells) and the degree of enlargement of these cells bear a rather constant relation to each other and both progressively increase as fruit size increases.

Fruit size at maturity is therefore related both to cell number and to cell size. Up to flowering the differences are all in cell number, for cell size is almost constant, the correlation between cell size and ovary size at flowering being only $+.0812 \pm .1760$. Final cell number is now established and is closely correlated with fruit size. However, the degree of cell enlargement is also related to mature fruit size, since cell expansion stops at progressively higher levels in the larger fruits with the result that there is a correlation of $+.9007 \pm .0020$ between cell size and fruit size at maturity. If cell number were the dominant factor in fruit size, the first part of the developmental curve would be as it is now, related to fruit size, and the

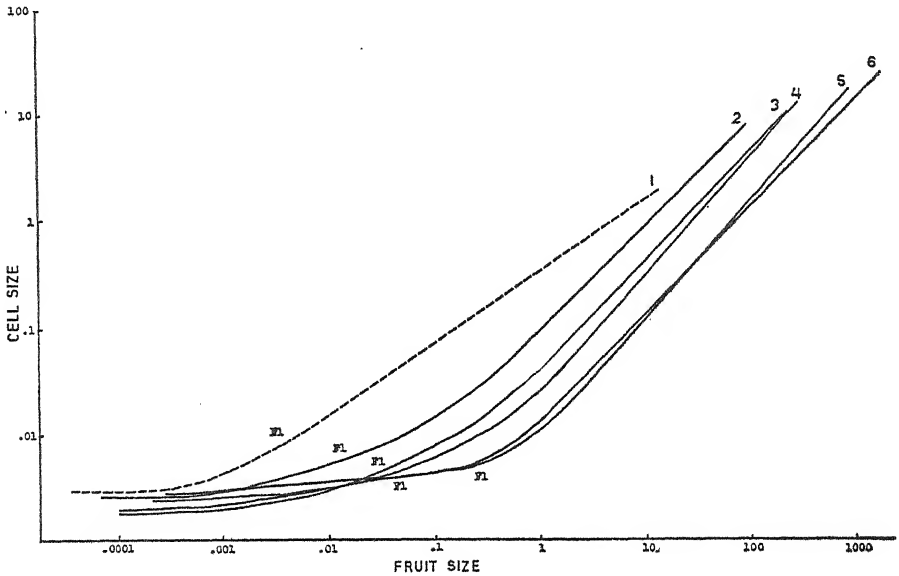

Fig. 2. Individual developmental curves for cell size plotted against fruit size, both logarithmically, in *L. pimpinellifolium* and in five types of *L. esculentum*. Line 1 (broken), *L. pimpinellifolium;* 2, Red Cherry; 3, Red Pear; 4, Red plum; 5, Red Peach; 6, Bonnie Best. *Fl*, size at flowering. Scale as in fig. 1.

second part would be of equal length in all types, reaching a uniform (and presumably optimum) cell size. If cell size were the dominant factor, the first part of the curve (cell number) would be uniform in all types and the second part would vary in extent. Neither of these conditions obtains, but the development of a particular size is the result of the combined action of both factors, cell size and cell number, acting in a specific and orderly fashion together. When this program has been completed growth stops. There is no obvious physiological reason why cell size in the Cherry type should not reach that attained by the Bonnie Best, but actually it stops

at about one third of this, at a point proportional to other points in development, such as the length of the meristematic period and the size at flowering.

We may conclude that size differences in the tomato fruits here studied are determined from the very beginning of development. The effect of these genetic differences is apparently upon an entire developmental program rather than upon any of its constituent factors.

SUMMARY

1. Seven pure breeding types of *Lycopersicum esculentum*, one type of *L. pimpinellifolium*, and fourteen F_1 progeny have been studied with respect to the development of fruit size and shape.

2. Shape differences develop by differential growth rates between polar and equatorial dimensions, established in the developing ovary primordium before flowering. After flowering the relative growth rate between dimensions is the same for all shape types.

3. The ultimate size of the fruit is determined very early in its development. Differences in size are visible in the floral primordia before differentiation of the ovary has begun and are maintained to maturity.

4. The early growth of tomato fruits is largely the result of cell multiplication; shortly before flowering the cells begin to enlarge and in *L. esculentum* all later growth is associated entirely with cell enlargement. This is not true for *L. pimpinellifolium* where some cell division continues up to maturity of fruit.

5. In all the varieties of *L. esculentum* the relationship between cell and organ size follows the same type of developmental program. Differentiation in size is associated with both the extent of cell division and the extent of cell enlargement.

The author wishes to thank Dr. E. W. Sinnott, under whose direction this work was done, for his assistance. Also she wishes to acknowledge a grant from the Herbert Maule Richards Memorial Fund of Barnard College which enabled her to pursue the problem.

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COLUMBIA UNIVERSITY

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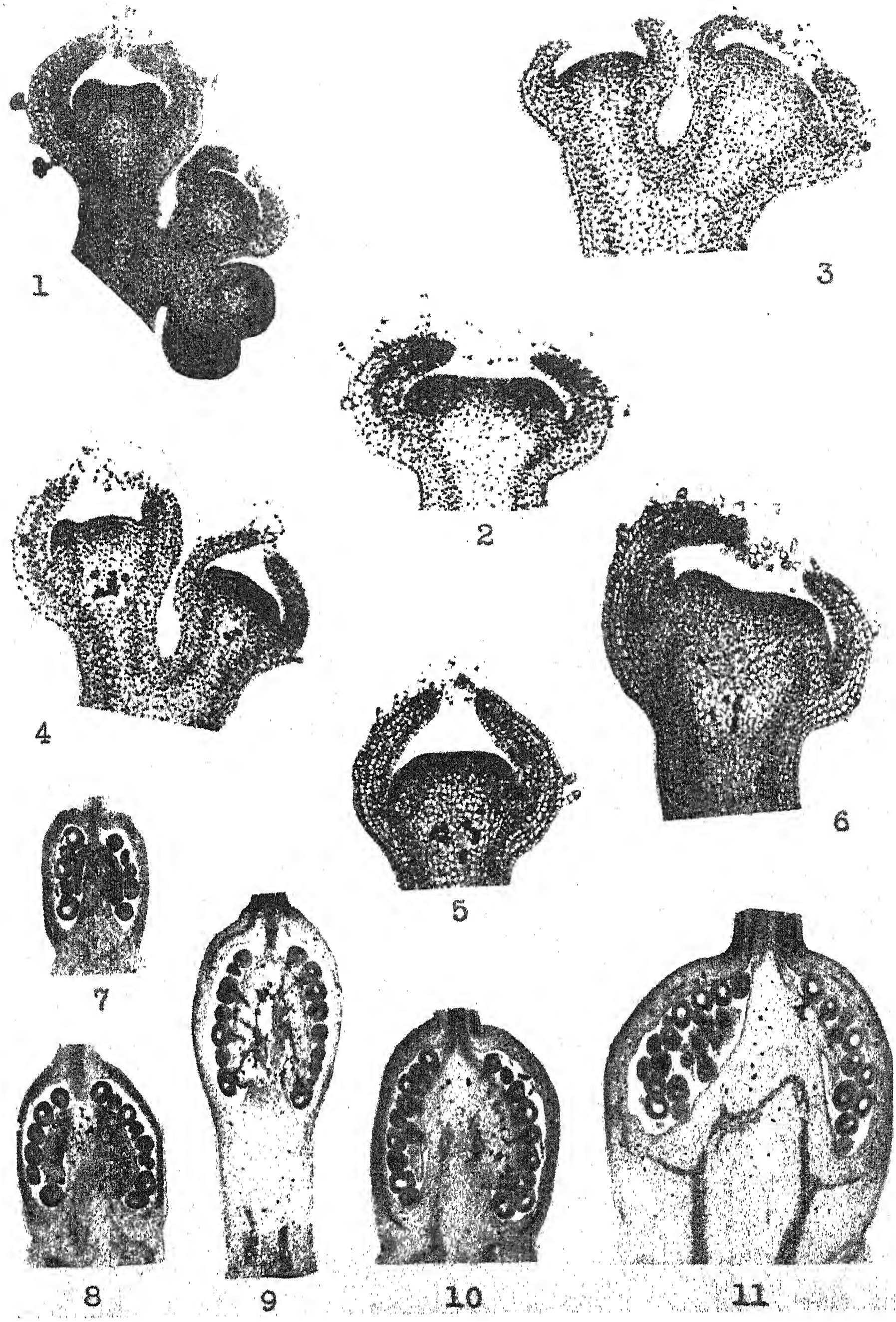
Explanation of plate 14

Figs. 1–6. Flower primordia, all ×90

1. Red Currant, *L. pimpinellifolium*
2. Bonnie Best×Red Cherry, *L. esculentum*
3. Red Peach
4. Red Cherry×Red Currant
5. Red Pear
6. Bonnie Best

Figs. 7–11. Ovaries at flowering, all ×20

7. Red Currant
8. Red Cherry
9. Red Pear
10. Red Peach
11. Bonnie Best



HOUGHTALING: TOMATO FRUITS

The genus Cheilophyllum of the West Indies

FRANCIS W. PENNELL

Some years ago, when studying the Cuban species of the family Scrophulariaceae, I realized that the little trailing plant which Grisebach had described as *Stemodia radicans* lacked the anther-structure peculiar to that genus; its closely contiguous cells showed that this species belonged with the more typical members of the tribe Gratioleae, although certain characters marked it as a distinct and rather remote genus. Accordingly in 1920 I established for it the new genus *Cheilophyllum*, so called from the Greek χειλος, margin, and φύλλον, leaf, in allusion to the thickened edges of the leaf-blades. Later, in my account of the "Scrophulariaceae of Cuba" (in Proc. Acad. Nat. Sci. Philadelphia **75**: 5. 1923), the position of the genus was shown in more detail by comparing it with others of this family in the Cuban flora.

The few collections seen did not suggest to me that *Cheilophyllum* could be other than monotypic, though occurring in both Cuba and Jamaica. But in 1931, in his study of Dr. E. L. Ekman's extensive collections, the late Dr. Ignatius Urban, after adopting my generic proposal, added four more species, all from Cuba. Despite my high regard for the opinion of the veteran student of the West Indian flora, I must confess that I was at first wholly skeptical about the validity of the new species. Thanks, however, to the receipt by the New York Botanical Garden of isotypes of three of the four species, supplied from the Natural History Museum at Stockholm, Sweden, I now gladly endorse all of Urban's proposed species, and must add yet three others, thus bringing the number in this genus to eight.

These little plants, which are so rarely collected, show considerable and seemingly constant differences between what appear to be well marked species. Most of these are known, however, from single or few collections, and the group should be revised again after the assembling of much more ample material. The following tentative outline is to show the present state of knowledge about this endemic Antillean genus.

Specimens have been reviewed in the following herbaria, each designated in the text by a symbol:

H—Gray Herbarium, Harvard University, Cambridge, Massachusetts;
Ph—Academy of Natural Sciences, Philadelphia, Pennsylvania;
Y—New York Botanical Garden, New York City.

CHEILOPHYLLUM Pennell

Cheilophyllum Pennell; Britton in Mem. Torrey Bot. Club 16: 103. 1920. Genotype, *Stemodia radicans* Griseb.

Corolla 5.5 mm. long; style 2.5 mm. long; leaf-blades elliptic or lanceolate, the thickened margin usually two-toothed. 1. *C. macranthum*
Corolla 1.5–3 mm. long; style 0.5–1 mm. long.
  Capsule ovoid, 2–2.5 mm. long, equaled or scarcely exceeded by the sepals; style 1 mm. long; leaf-blades elliptic to nearly circular, dentate.
    Leaf-blades oval or wider, with thickened recurved margins; sepals acute.
      Apex of the slightly margined leaf-blades obtuse or rounded; internodes less than twice the length of the leaves; plant somewhat pubescent.
        Leaf-blades widely oval or nearly circular, broadly rounded, pubescent and obscurely punctate beneath, 3–5 mm. long; stem, pedicels, and sepals pubescent, the hairs obscurely or not glandular; stems long, little branched, 10–20 cm. long. 2. *C. radicans*
        Leaf-blades oval, obtuse or somewhat rounded, glabrous and prominently punctate beneath, 2–4 mm. long; stem glabrous; pedicels, and especially sepals, sparsely glandular-pilose; stems shorter, much branched, only 3 to 5 cm. between plantlets. 3. *C. microphyllum*
      Apex of leaf-blades acute; internodes 2 to 4 times the length of the leaves.
        Stem and leaves glabrous, the latter strongly margined; pedicels 4–6 mm. long; internodes 3 to 4 times the length of the leaves. 4. *C. marginatum*
        Stem glandular-pubescent; leaves with midrib somewhat pubescent beneath, the blades only slightly margined; pedicels 2–3 mm. long; internodes usually the length of the leaves. 5. *C. jamaicense*
    Leaf-blades elliptic, the margin slightly, if at all, thickened or recurved; sepals attenuate, glandular-pilose. 6. *C. dentatum*
  Capsule short-ovoid or globose, 1–1.5 mm. long, exceeded by the sepals; style 0.5–0.7 mm. long; leaf-blades elliptic or elliptic-lanceolate, entire or nearly so.
    Pedicels 3–4 mm. long, shorter than or equaling the bracts; leaf-blades 4–5 mm. long; sepals and pedicels glandular-pubescent. 7. *C. micranthum*
    Pedicels 5–8 mm. long, exceeding the bracts; leaf-blades 3–4 mm. long; sepals and pedicels sparsely glandular-pilose or glabrate. 8. *C. sphaerocarpum*

1. CHEILOPHYLLUM MACRANTHUM Urban.

Cheilophyllum macranthum Urb. in Arkiv Bot. 23A. n. 11: 39. 1931. "Cuba, prov. Santa Clara prope Mordazo ad Laguna Yaiti, . . . [E. L. Ekman] n. 17104." Type not seen nor verified, but apparently well distinguished by its large flower; the fruit is still unknown.

Middle Cuba.

CUBA. Santa Clara: Mordazo, Ekman 17104.

2. CHEILOPHYLLUM RADICANS (Grisebach) Pennell.

Stemodia radicans Griseb., Cat. Pl. Cub. 182. 1866. "Cuba occ. (Wr[ight] 3006), in savannis pr[ope] Hanabana (Wr[ight] a-1865)." Isotypes of Wright 3006 have

been seen in Gray Herbarium and New York Botanical Garden; at the former accompanied by penciled descriptive and locality notes, the latter being "sandy pinales. Dec. 2. Asiento viejo to Remates." At both institutions Wright 3006 contains two species intermixed, the present and the following, but the sheet that bears this geographic information bears only the present species. These localities are in Pinar del Rio, and nearly at the western extremity of Cuba. While the description was based upon both components, it was clearly the long, repeatedly rooting stems of the present plant that suggested the specific name. The plant from Hanabana appears to be lacking in American herbaria.

Sandy pineland, western Cuba.

CUBA. Pinar del Rio: Asiento viejo to Remates, C. Wright 3006 p.p. (H,Y).

3. **Cheilophyllum microphyllum** Pennell, sp. nov.

Stems strongly ridge-angled, glabrous, much branched, only 3 to 5 cm. long between plantlets. Leaf-blades 3–4 mm. long, oval, acutish to somewhat rounded, slightly crenately dentate, glabrous, glandular-punctate, narrowed to sessile or shortly petiolar bases, the margin slightly incurved and callose-thickened. Pedicels 2–4 mm. long, slightly glandular-pilose. Sepals 1.5–2 mm. long, lanceolate, attenuate, finely glandular-pubescent. Corolla 3 mm. long, white, the tube slightly pubescent within, the lobes slightly longer than the tube, the posterior wider, nearly distinct or much united. Anthers 0.3 mm. long. Style 1 mm. long. Capsule 2–2.5 mm. long, ovoid, acute. Seeds not seen.

(Caulis ramosissimus, glaber; folia 3–4 mm. longa, ovalia, obtusa, dentata, glabra, punctata, margine paulum incrassata; pedunculi 2–4 mm. longi; sepala 1.5–2 mm. longa, minute glandulo-pilosa; corolla 3 mm. longa; capsula 2–2.5 mm. longa, ovoidea, acuta.)

Type, western Cuba ("Cuba occ."), collected in flower and fruit by Charles Wright, no. 3006 p.p., in Gray Herbarium of Harvard University; isotypes in Herb. New York Botanical Garden and Academy of Natural Sciences of Philadelphia.

Western Cuba.

CUBA. Pinar del Rio, Wright 3006 p.p. (H,Ph,Y).

4. **Cheilophyllum marginatum** Pennell, sp. nov.

Stems strongly ridge-angled, glabrous, little branched above base, reaching 10 to 15 cm. long. Leaf-blades 3–5 mm. long, oval, acute, distally with one or two pairs of more or less sharp teeth, relatively glabrous, strongly glandular-punctate, narrowed to shortly petiolar bases, the margin strongly incurved and callose-thickened. Pedicels 4–6 mm. long, very sparsely glandular-pilose. Sepals 2–2.5 mm. long, linear-lanceolate, glabrous. Corolla 2.5 mm. long, white, the tube slightly pubescent within, the lobes slightly longer than the tube, the posterior little if at all wider, and apparently only partially united beyond the others. Anthers 0.3 mm. long. Style about 1 mm. long. Capsule 2.5 mm. long, ovoid, acute. Seeds 0.3 mm. long, 0.2 mm. wide, brownish-black, minutely ridged.

(Caulis paulum ramosus, glaber; folia 3–5 mm. longa, ovalia, acuta, dentata, glabrata, punctata, margine forte incrassata; pedunculi 4–6 mm. longi; sepala 2–2.5 mm. longa, glabra; corolla 2.5 mm. longa; capsula 2.5 mm. longa, ovoidea, acuta.)

Type, Placetas del Sur, Santa Clara, Cuba, collected in flower and fruit August 10, 1918 by Bro. Leon and Ter. M. Roca, no. 8150; in Herb. New York Botanical Garden.

Middle Cuba.

CUBA. Santa Clara: Placetas del Sur, Leon & Roca 8150 (Y); Sagua, N. L. Britton & P. Wilson 330 (Y).

5. **Cheilophyllum jamaicense** Pennell, sp. nov.

Stems ridge-angled, minutely glandular-pubescent, much branched at base, the branches reaching 15 to 25 cm. long. Leaf-blades 4–7 mm. long, oval, acute, with one or two pairs of rounded or rather sharp teeth, glabrous except on the midrib beneath, glandular-punctate, cuneately narrowed to sessile or scarcely petiolar bases, the margin incurved and slightly callose-thickened. Pedicels 2–3 mm. long, glandular-pubescent. Sepals 2.5 mm. long, lanceolate, glandular-pubescent. Corolla white, seen only in bud. Style 0.7 mm. long. Capsule 2 mm. long, ovoid, acute. Seeds not seen.

(Caulis pubescens, ramosissimus; folia 4–7 mm. longa, ovalia, acuta, dentata, glabrata, punctata, margine incrassata; pedunculi 2–3 mm. longi; sepali 2.5 mm. longa, pubescentia; capsula 2 mm. longa, ovoidea, acuta.)

Type, growing in shade of grasses, Ashley Hall Savanna, Lower Clarendon, Jamaica, alt. 100 ft. (30 m.), collected in flower and fruit December 6, 1917, by William Harris, no. 12737; in Herb. New York Botanical Garden.

Grassland, Jamaica.

JAMAICA. Lower Clarendon: Ashley Hall Savanna, Harris 12737 (H,Ph,Y).

6. Cheilophyllum dentatum Urban.

Cheilophyllum dentatum Urb. in Arkiv Bot. **23A**. n. 11: 41. 1931. "Cuba, prov. Santa Clara prope Motembo in savannis humidis, . . . [Ekman] n. 16810." Isotype, collected June 27, 1923, seen in Herb. New York Botanical Garden.

Grassland, middle Cuba.

CUBA. Santa Clara: Motembo, Ekman 16810 (Y).

7. Cheilophyllum micranthum Urban.

Cheilophyllum micranthum Urb. in Arkiv Bot. **23A**. n. 11: 40. 1931. Cuba, prov. Camaguey ad kilom. 9 lineae ad Nuevitas versus in Carrascales (v. Cuabales). . . . [Ekman] n. 15567." Isotype, collected October 21, 1922, seen in Herb. New York Botanical Garden.

Middle Cuba, Carrascales.

CUBA. Camaguey: at km. 9 of the line to Nuevitas, Ekman 15567 (Y).

8. CHEILOPHYLLUM SPHAEROPHYLLUM Urban.

Cheilophyllum sphaerocarpum Urb. in Arkiv Bot. **23A**. n. 11: 39. 1931. "Cuba, prov. Santa Clara prope Motembo in palmetis, . . . [Ekman] n. 16826." Isotype, collected June 27, 1923, seen in Herb. New York Botanical Garden.

Gravelly soil, along streams and in palm groves middle Cuba.

CUBA. Santa Clara: Motembo, Ekman 16826 (Y); Sabana de Motembo, Bro. Leon & A. Loustalat 9361 (Y), 11341 (Ph,Y).

ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA

The anatomy of the stem in the Lejeuneae

ALEXANDER W. EVANS

(concluded)

Paradoxae

COLURA ORNATA Goebel. In the genera *Colura* and *Diplasiolejeunea* the underleaves are duplicate; that is, there is one underleaf for every lateral leaf, instead of one for every two lateral leaves, as in the Holostipae and Schizostipae. In spite of this peculiar feature both genera show the simplified type of stem-structure found in the last four of the Schizostipae under consideration. In other words the cortical cells are in seven longitudinal rows and the medullary cells in three. The genus *Colura* is largely tropical and includes many epiphyllous species, of which the East Indian *C. ornata* is a characteristic example. The irregularly branched stems of this pale green plant are mostly 1–2 cm. in length, about 0.1 mm. in width, and about 0.06 mm. in thickness. Cross-sections, in consequence, are elliptical (fig. 7, A). The cortical cells measure 25–40μ width by 15–30μ in thickness, and those of the two ventral rows are distinctly smaller than the others. The medullary cells average about 25μ in diameter. The unpigmented cell-walls are thin or slightly thickened, and the bounding walls may be as much as 4μ thick. In the interior indistinct triangular thickenings can be demonstrated where three cells come together.

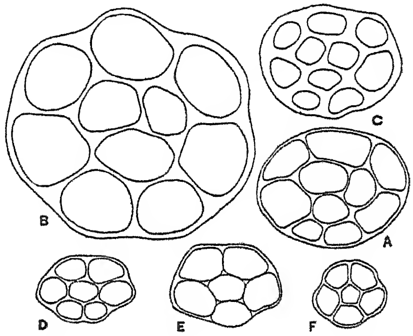


Fig. 7. Cross-sections of stems. A *Colura ornata* Goebel. B. *Diplasiolejeunea unidentata* (Lehm. & Lindenb.) Schiffn. C. *D. pellucida* (Meissn.) Schiffn. D. *Leptocolea planifolia* Evans. E. *L. scabriflora* (Gottsche) Evans. F. *Aphanolejeunea microscopica* (Tayl.) Evans. All, ×225.

DIPLASIOLEJEUNEA UNIDENTATA (Lehm. & Lindenb.) Schiffn. Except for a few extra-tropical species the genus *Diplasiolejeunea* is tropical and includes both corticolous and epiphyllous representatives. The West Inian *D. unidentata* may be chosen as an example of the first group The pale green plants of this rather robust species form irregular or radiating patches, and the sparingly pinnate stems, which are about 0.14 mm. in diameter, may attain a length of 2.5 cm. The cell-walls, as seen in cross-section, show a pale brownish yellow pigmentation. The cortical cells (fig. 7, B) measure 40–50μ in width and thickness, and the medullary cells average

about 35μ in diameter. The outer walls of the stem are 6–8μ thick, but the other walls are mostly only 3–4μ thick, except for the more or less distinct triangular thickenings, wherever three cells come together.

DIPLASIOLEJEUNEA PELLUCIDA (Meissn.) Schiffn. The present species, which is representative of the epiphyllous forms of the genus, has a wide distribution in tropical America and is known also from Africa. Although the irregularly branched, pale green plants may be as much as 2 cm. in length, they are more delicate than in *D. unidentata*, and the stems average only 0.085 mm. in width by 0.06 mm. in thickness. The cortical cells (fig. 7, C) are 25–30μ in width by 15–20μ in thickness, and their walls are 4–6μ thick. The medullary cells average about 20μ in diameter, and their walls are nearly or quite as thick as those of the cortical cells. All the walls are cream color and are uniformly thickened, except for occasional pits in the medulla.

In the various stems having seven rows of cortical cells and three rows of medullary cells, the relations of symmetry are of considerable interest. Favorable cross-sections, such as the one represented in figure 7, B, show that the dorsal cortical cell is in contact with two medullary cells, that the adjoining lateral cortical cells are each in contact with a single medullary cell, that the succeeding lateral cortical cells are each in contact with two medullary cells, and that the two ventral cortical cells are each in contact with a single medullary cell. If these relationships are kept in mind it will be seen that the only axis of symmetry is a vertical line passing through the middle of the dorsal cortical cell, between the two lateral medullary cells, through the middle of the ventral medullary cell, and between the two ventral cortical cells. These highly simplified stems, therefore, exhibit bilateral symmetry only and thus differ from the more generalized type of stem found in *Taxilejeunea pterogonia*, in which a radial symmetry has been demonstrated.

LEPTOCOLEA PLANIFOLIA Evans. The genus *Cololejeunea*, as originally defined, included all the Lejeuneae without underleaves. In place of these structures the ventral segments of the stem develop radicelliferous cells or groups of cells, which have the power of growing out into rhizoids. As pointed out by Goebel (1928, p. 25) the radicelliferous cells or groups of cells are duplicate, just as the underleaves are duplicate in *Colura* and *Diplasiolejeunea*. The absence of underleaves, which in itself indicates an advanced stage of development from the standpoint of evolution, is associated with the most highly simplified, or advanced, type of stem-structure to be found in the Lejeuneae. The stems, in other words, have only five or six rows of cortical cells and only a single row of medullary cells. The rows

of cortical cells include two on each side in a lateral (or dorsi-lateral) position and one or two in a ventral position. In certain cases the number of ventral rows may be increased to three in the vicinity of the radicelliferous cells, but the normal number for a given species is one or two.

During recent years several groups of species have been separated from *Cololejeunea* as distinct genera, and *Leptocolea* represents one of these segregates. It is composed of corticolous and epiphyllous species, most of which are tropical, and includes some of the more robust Lejeuneae without underleaves. In spite of this fact the species of *Leptocolea* are delicate and fragile. The pale green plants of *L. planifolia*, a Porto Rican species, form depressed mats on living leaves. The individual stems are irregularly branched and measure, in most cases, 0.5–1 cm. in length, about 0.06 mm. in width, and about 0.045 mm. in thickness. The lateral cortical cells (fig. 7, D) are 20–25μ in width by 12–20μ in thickness. The ventral cortical cells, which may be a little smaller, are normally in two rows. In the vicinity of the radicelliferous cells, however, an additional row may be present and on slender branches the number of rows may be reduced to one. The medullary cells are about 20μ in diameter. The unpigmented cell-walls are thin or slightly thickened, but the thickness rarely exceeds 2μ.

LEPTOCOLEA SCABRIFLORA (Gottsche) Evans. This epiphyllous species is widely distributed in tropical America, particularly in Brazil. The pale green, sparingly branched stems, which grow scattered or in depressed mats, are about 1 cm. long, 0.05 mm. in width, and 0.04 mm. in thickness. The cortical cells, which are in five rows (fig. 7, E), are mostly 14–20μ in width by 10–14μ in thickness, and the medullary cells average about 14μ in diameter. The bounding walls of the lateral cortical cells are 2–3μ thick, but all the other walls are thin, except for minute triangular thickenings at the angles.

APHANOLEJEUNEA MICROSCOPICA (Tayl.) Evans. The genus *Aphanolejeunea* is another segregate from the genus *Cololejeunea* as originally defined. The species are minute and delicate and grow for the most part on bark and living leaves. Although the genus is largely tropical the type-species, *A. microscopica*, is known only from a few scattered localities in western Europe, where it grows on rocks and trees, usually in company with other hepatics. The fragile pale green stems, which branch sparingly, rarely exceed 0.5 cm. in length and average about 0.04 mm. in diamteer. The cortical cells, four rows of which are lateral and one ventral (fig. 7, F), bulge slightly and measure about 20μ in width by 15μ in thickness. The medullary cells average about 10μ in diameter, and the colorless cell-walls are all about 2μ thick.

In such species as *Leptocolea scabriflora*, in which a certain amount of dorsiventral flattening is apparent in the stem, the vertical median plane is the only plane of symmetry present, and the stem is therefore a bilateral organ, comparable in this respect with the stems of *Microlejeunea bullata*, *Diplasiolejeunea unidentata*, and other species having seven rows of cortical cells and three rows of medullary cells. In such species as *Aphanolejeunea microscopica*, however, in which there is no dorsiventral flattening of the stem, each plane passing through a row of cortical cells and between the opposite pair of rows is a plane of symmetry. There are therefore four oblique planes of symmetry in addition to the vertical plane, making five in all. The stem in consequence is a radial organ, comparable with the stems of *Taxilejeunea pterogonia* and similar forms with seven planes of symmetry.

In the writer's experience the stems of *Leptocolea scabriflora* and *Aphanolejeunea microscopica* are representative of the most simplified types of stem-structure found in the Lejeuneae. Goebel, however, has described a still more simplified type in a Sumatran species of *Aphanolejeunea*, to which he has given the name *Physocolea* (*Aphanolejeunea*) *proboscoidea* (1928, p. 38). In the normal stem of this species, according to his account, there are only three rows of cortical cells surrounding the axial row of medullary cells; and it is further stated that the medullary row may be absent and that the stem, under these circumstances, consists of three longitudinal rows of cells meeting in the axis.

It is unfortunate that Goebel did not figure cross-sections of these simplified stems. The figure which he cites as illustrating the normal type of structure (1928, *pl. 6, f. 63*) need not necessarily be interpreted in the way he suggests. The figure in question represents the ventral surface of a stem, and the three rows of cells shown are the ventral row of cortical cells (with the radicelliferous cells clearly indicated) and a lateral row of cortical cells on each side. A stem with five rows of cortical cells would present the same appearance, since the two lateral rows meeting in the middle of the dorsal surface would be concealed by the two rows shown. His other figures of stems, which represent a closely allied species (1928, *pl. 6, f. 68, 70, 71*), might equally well have been drawn from stems with five rows of cortical cells. It may be recalled that Leitgeb described and figured very young stems of *Trichocolea tomentella* (Ehrh.) Dumort. and *Chiloscyphus pallescens* (Ehrh.) Dumort., in which cross-sections showed only three cells meeting in the center (1875, p. 6, footnote; *pl. 3, f. 18c; pl. 6, f. 16b*). These stems, however, were so young that rudimentary leaves had not yet made their appearance, and with the appearance of leaves the arrangement of the cells in the stem at once became more complicated. This was brought

about by the cutting off of medullary cells and by an increase in the number of the outside cells, now representing the cortex. It would hardly be expected that the stem of one of the Lejeuneae, with its highly specialized, complicate-bilobed leaves, could be simplified to such an extent that these leaves would arise from a single row of cells, although cases are known where they arise from two rows, one of which gives off the lobe and the other the lobule. It is of course possible that Goebel's observations may have been made on stems which were still in a juvenile stage of development, but in any case the confirmation of his statements is much to be desired.

GENERAL DISCUSSION

Various features of the Lejeuneae indicate that the group is relatively "advanced" from the standpoint of evolution. In a group of this character, which contains many diverse elements, it is exceedingly difficult to interpret the details of stem anatomy in terms of phylogenetic relationship, although certain evolutionary trends can be distinguished more or less clearly. It is perhaps safe to assume, in a broad way, that the more generalized types preceded the more specialized types, and that the latter arose through processes of differentiation or reduction or perhaps through combinations of the two. Few students, for example, would maintain that the highly simplified stems found in the Paradoxae and in many of the Schizostipae represent primitive conditions. They represent, rather, advanced conditions in which the process of reduction has proceeded toward an extreme limit.

The more generalized types of stems in the Hepaticae are those in which the differentiation into tissues is slight and in which the component cells are numerous and irregular in their arrangement. If these criteria are applied to the Lejeuneae it will be seen that the stems of certain Holostipae conform more or less closely to the generalized condition. In *Neurolejeunea Breutelii*, for example, cross-sections of stems (fig. 3, C) bring out very slight differences between the cortical and medullary cells, and the same thing is true of *Omphalanthus filiformis* (fig. 3, H). Both cortex and medulla, moreover, are composed of an indefinite but fairly large number of cells, and the arrangement of these cells tends to be irregular. Macerated preparations (fig. 3, D–G, I–N), to be sure, show that the differences between the cortical and medullary cells are greater than the cross-sections indicate; but, even so, these stems approach the theoretically generalized condition more closely than those of most Lejeuneae.

Passing from the more generalized types of stem-structure, two divergent lines of evolutionary advance can apparently be recognized, one leading to more complex and more highly differentiated conditions and the

other to more simplified conditions. The stems of such species as *Bryopteris filicina* (fig. 1) and *Ptychanthus striatus* (fig. 2) exemplify the first line of advance. In these stems the number of component cells, in comparison with the *Neurolejeunea* and the *Omphalanthus*, is greater, the differences between the cortical and medullary cells are more pronounced, and the medulla itself is differentiated into various kinds of cells. These stems, it will be remembered, maintain in the air a more or less horizontal position and are thus exposed to unusual conditions. Their increased size and more marked differentiation must help them in withstanding the environmental dangers to which they are subjected, and the teleologist might explain their complex structure on the basis of adaptation. However this may be, the stems in question apparently represent an advance from a more generalized condition, although the possibility of a progress in the opposite direction can not be altogether ignored.

In the evolutionary advance toward simplification, an increase in the size of the cortical cells, accompanied in most cases by a decrease in their number, may be looked upon as an initial step. The stems of *Brachiolejeunea insularis* (fig. 5, A), *Dicranolejeunea axillaris* (fig. 5, B), and *Odontolejeunea lunulata* (fig. 5, D) illustrate this condition clearly. The cortical cells in these stems are distinctly larger than the medullary cells and, in the *Dicranolejeunea* and the *Odontolejeunea* at least, are arranged in only ten longitudinal rows. In *Anoplolejeunea conferta* (fig. 5, E) the process of reduction has gone a little farther, and only seven rows of cortical cells are present. It has already been pointed out that seven rows of cortical cells are to be found in the vast majority of the Schizostipae, as well as in the Paradoxae with underleaves.

The stems of the Schizostipae, if the group is taken as a whole, are more simplified or advanced than those of the Holostipae. Not only is this the case but the process of reduction can be clearly followed within the group. In doing this the very few species with more than seven cortical cells, such as *Potamolejeunea orinocensis* (fig. 6, A), may be left out of consideration, and such a species as *Taxilejeunea pterogonia* (fig. 6, B), with seven rows of cortical cells and a large, well-differentiated medulla, may be chosen as having a relatively primitive type of stem-structure. Starting with such a stem it will be found that the reduction has not involved the number of cortical cells but has involved, in a marked degree, the number of medullary cells. In *Taxilejeunea pterogonia*, for example, about thirty-five medullary cells appear in cross-sections of the stems; in *Cystolejeunea lineata* (fig. 6, I), however, only about twenty-five are present, in *Hygrolejeunea cerina* (fig. 6, H) about twenty, in *Lejeunea flava* (fig. 6, L) about thirteen, and in *Pycnolejeunea macroloba* (fig. 6, K) about eleven. The proc-

ess of reduction within the group reaches its ultimate stage in such species as *Drepanolejeunea inchoata* (fig. 6, O), *Leptolejeunea elliptica* (fig. 6, P), and *Microlejeunea bullata* (fig. 6, N), in which cross-sections show only three medullary cells.

The type of stem-structure illustrating the ultimate stage of reduction in the Schizostipae corresponds with the primitive type of structure in the Paradoxae. This is found in forms with underleaves, and is exemplified by such species as *Colura ornata* (fig. 7, A), *Diplasiolejeunea unidentata* (fig. 7, B), and *D. pellucida* (fig. 7, C). As already pointed out, however, the reduction has proceeded still farther in forms without underleaves and has involved both cortical and medullary cells. In *Leptocolea scabriflora* (fig. 7, E) and *Aphanolejeunea microscopica* (fig. 7, F), for example, cross-sections of stems show only five cortical cells surrounding a single medullary cell.

It may be noted that the cell-differentiation, which is so pronounced in some of the more complex stems of the Holostipae and Schizostipae, tends to become less so as the process of reduction goes on. This may be illustrated by such a series as *Taxilejeunea pterogonia*, *Hygrolejeunea cerina*, *Lejeunea flava*, *Leptolejeunea elliptica*, and *Aphanolejeunea microscopica*. In the last two members of this series the histological differences between the cortical and medullary cells are very slight.

The stems of the Lejeuneae perform various physiological functions and exhibit, in varying degrees, a division of labor. The process of absorption, for example, even in the most simplified stems, is carried on by the cortical cells; and it has already been pointed out that these cells, in stems with a large-celled cortex (see, for example, page 202), may represent also an important photosynthetic tissue, with the storage of water as a possible subsidiary function.

In the smaller and more simplified stems the most important functions are undoubtedly absorption and photosynthesis. In larger and more complex stems, however, the maintenance of rigidity and the transportation of aqueous solutions become increasingly important. This is particularly true of such species as *Bryopteris filicina* (fig. 1), *Ptychanthus striatus* (fig. 2), and *Stictolejeunea Kunzeana* (fig. 3, A), in which relatively large branch-systems, spreading out horizontally in the air, are produced. In the stems of these species the peripheral medullary cells are characterized by their fiber-like form, very thick walls and small lumina. Cells of this character, by their structure and position, are clearly of use in resisting bending forces. They are associated with similar thick-walled cells having thin oblique or transverse walls at the ends. Such cells supplement the fiber-like cells as skeletal elements and, at the same time, afford facilities for the transportation of solutions in a longitudinal direction.

Although the thick-walled cells in the species just discussed are significant as supporting structures, there are other species with thick-walled cells in which the stems are scarcely or not at all exposed to bending or crushing forces. The species in question have prostrate stems, closely adherent to the substratum or growing in depressed mats. As examples *Omphalanthus filiformis* (fig. 3, H), *Leucolejeunea xanthocarpa* (fig. 3, O), and *Pycnolejeunea macroloba* (fig. 5, K) might be cited. What is the significance of the thick cell-walls in such cases? In the opinion of Goebel (1915, p. 553) thick cell-walls in the bryophytes owe their chief value to their power of absorbing water rapidly by imbibition. He therefore looks upon them as a xeromorphic feature, whereby the plants possessing them are enabled to resume their physiological activities quickly and effectively after periods of dryness. In opposition to this view it might perhaps be urged that many of the Lejeuneae and other bryophytes with thick cell-walls grow in habitats which are well supplied with water, rather than in dry habitats. Even in favorable localities, however, periods of abundant water-supply may be interrupted by periods of dryness, during which plants growing in exposed situations may be subjected to xerophytic conditions. Since these plants are unprovided with cuticular coverings of any sort they tend to lose much of their water and to pass quickly into a condition of inactivity. This is the case with the Lejeuneae under consideration. Their thick cell-walls, therefore, might well have the significance which Goebel would assign to them.

THE RELATIONSHIP BETWEEN THE SEGMENTS AND THE ADULT STEM

In the development of the shoot the Holostipae and Schizostipae conform to the type which is found in the vast majority of the acrogynous Jungermanniales. In this type the development is by means of an apical cell with three cutting faces, two of which are lateral and the third ventral. The segments cut off from the apical cell are parallel with these faces and arise in a spiral sequence (fig. 8, E). In other words a ventral segment is followed by a lateral segment on one side, then by a lateral segment on the other side, then by a second ventral segment, then by a second lateral segment on the first side, and so on. Each segment, by means of subsequent growth and cell-division, gives rise to a definite portion of the adult shoot. This may be designated a merophyte, as suggested by Douin (1925, p. 575), and the adult shoot in consequence is composed of three longitudinal rows of merophytes, two of which are lateral and the third ventral.

In the Paradoxae an important deviation from the course of development just described is met with. Although the apical cell in this group has three cutting faces, although two of these faces are lateral and one ven-

tral, and although the apical cell cuts off segments parallel with these faces, the segments do not arise in a spiral sequence but in what Goebel called a pendular sequence. In other words a ventral segment is followed by a lateral segment on one side, then by a second ventral segment, then by a lateral segment on the other side, then by a third ventral segment,

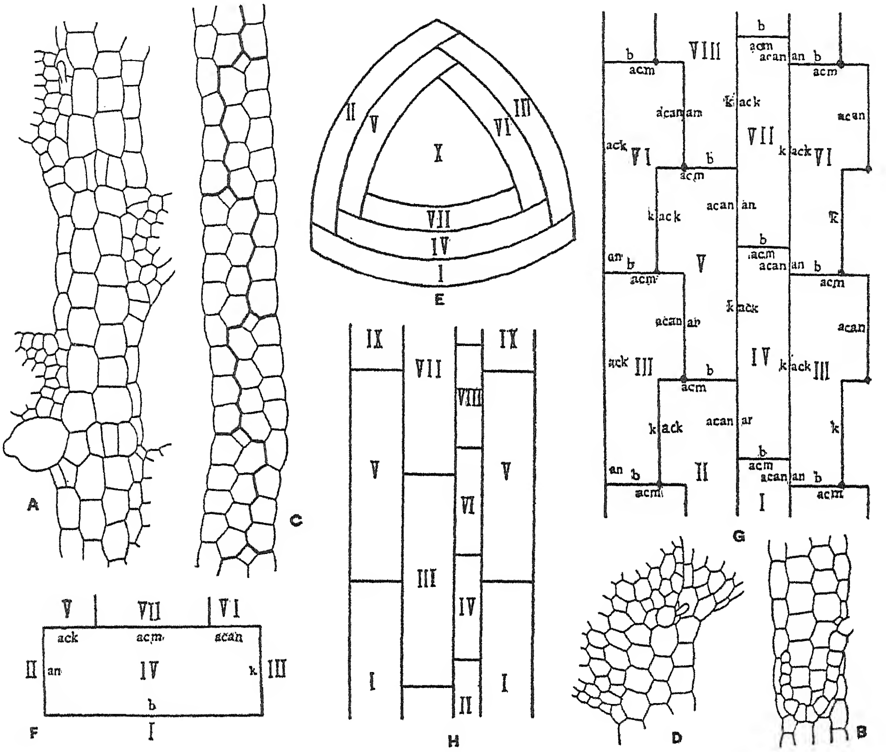


Fig. 8. A–D. *Lejeunea flava* (Swartz) Nees. A. Ventral view of stem, with underleaves dissected away, ×100. B. Lateral view of stem, showing attachment of a leaf, ×100. C. Dorsal view of stem, with leaves dissected away, ×100. D. Base of leaf, dorsal view, ×100. E–H. Diagrams. E. Apical cell and young segments cut off in a dextrorse spiral sequence. F. A single ventral segment. G. Superficial boundaries of merophytes in *L. flava*. H. Superficial boundaries of merophytes in *Aphanolejeunea microscopica* (Tayl.) Evans.

then by a second lateral segment on the first side, then by a fourth ventral segment, and so on. Goebel first associated the pendular sequence with the genus *Colura* (see 1915, p. 588), but it is found also in *Diplasiolejeunea* and *Cololejeunea*, as well as in the segregates from the latter genus (see Goebel, 1928, p. 26). In this type of development the merophytes are still arranged in three longitudinal rows, two of which are lateral and the third

ventral, but the ventral row has twice as many merophytes as either of the lateral rows.

Each lateral merophyte bears a leaf and each ventral merophyte an underleaf, if the species under consideration has underleaves. In the Holostipae and Schizostipae, therefore, there are just as many underleaves as there are leaves in each lateral row, but in the Paradoxae with underleaves there are twice as many. In the Paradoxae without underleaves the position of the latter is marked by the presence of radicelliferous cells or groups of cells.

If it is assumed that the stem is a cylindrical organ, the cauline portion of each merophyte will be, at least theoretically, in the form of a sector of a cylinder (see Douin, 1925, *pl. 8, f. 18*), and this will be true whether the sequence in the cutting off of the segments is spiral or pendular. The three rows of merophytes, moreover, will meet in the axis of the stem, the two lateral rows will meet in a plane extending from a median longitudinal line on the dorsal surface to the axis, the ventral row will meet the lateral rows in similar planes extending from the ventral surface to the axis, and a cross-section of the stem will be in the form of a circle divided into three sectors, each representing the cross-section of a merophyte. It may be added that the surface of each merophyte, if spread out flat, would have a rectangular outline.

Of course the theoretical forms and relationships of the merophytes, which have just been described, are rarely, if ever, completely realized in the Lejeuneae or in any other group of the leafy hepatics. This is due in part to irregularities in the sequence of cell-divisions in the developing merophytes, in part to displacements and readjustments of cell-walls whereby the boundaries of the merophytes are obscured, and in part to other causes. At the same time a more or less close approximation to the theoretical condition can, in many cases, be demonstrated. This will become evident from the study of *Lejeunea flava* which may be considered representative of the Schizostipae.

Leitgeb's important studies on the leafy hepatics (1871, 1875) are of great help in interpreting the conditions found in *L. flava*. According to the nomenclature suggested by Nägeli and Leitgeb (see 1867, p. 77) each segment cut off from the apical cell is bounded by the following five walls: the free wall, the basiscopic wall, the kathodic wall, the acroscopic wall, and the anodic wall. In the accompanying diagram (fig. 8, E), which represents an apical cell (x) and a series of segments cut off in a dextrorse spiral sequence, the ventral segment IV may be taken as an illustrative example. For the sake of clearness this segment is represented also by itself (fig. 8, F) and it will be seen that the basiscopic wall (b) separates

the segment from segment I, the anodic wall (*an*) from segment II, the acroscopic wall from segments V, VII, and VI, and the kathodic wall (*k*) from segment III. Segment IV, therefore, is in contact with six other segments, and the merophyte developing from segment IV will be in close union with the merophytes developing from these segments, so far as their cauline portions are concerned. Of course the outline of the diagram represents the free wall of segment IV.

Although the free wall of a segment and the free surface of the merophyte developing from it are both approximately rectangular, the lower end of the merophyte is the only part that corresponds with one of the walls of the original segment. This was definitely demonstrated by Leitgeb (1871) in the case of the ventral segments and young ventral merophytes of *Radula complanata* (L.) Dumort., a species without underleaves. According to his account the basiscopic wall of the segment remains straight and gives rise to the lower end of the merophyte. The acroscopic wall, however, although at first straight, does not remain so, owing to changes that take place in the portions of the wall separating the segment from the two next younger segments. In segment IV (fig. 8, F) the portions in question are the kathodic portion (*ack*), separating the segment from segment V, and the anodic portion (*acan*), separating the segment from segment VI. As growth proceeds these portions gradually bend backward and finally assume a longitudinal direction, becoming continuous with the anodic and kathodic walls, respectively, of the segment. In this process the kathodic portion becomes longer than the anodic portion (as shown by Leitgeb's *pl. 11, f. 3 B*). Through the bending backward of the kathodic and anodic portions of the acroscopic wall, the only portion left to form the upper end of the merophyte is the median portion (*acm*), which separates segment IV from segment VII. It follows further that one side of the merophyte is derived from the anodic wall and the kathodic portion of the acroscopic wall of the segment, whereas the other side is derived from the kathodic wall and the anodic portion of the acroscopic wall. Since the free surface of the merophyte is rectangular the part derived from the kathodic wall must be longer than the part derived from the anodic wall.

The relationships demonstrated by Leitgeb in the ventral merophytes of *Radula complanata* are exhibited just as clearly in the ventral merophytes of *Lejeunea flava*, although each merophyte in the latter species bears an underleaf at the upper (or acroscopic) end. This is brought out by figure 8, A, which represents in ventral view a portion of a stem from which the underleaves have been dissected away. Since the spiral sequence in the selected example is dextrorse, the anodic sides of the merophytes are on the left and the kathodic sides on the right. The upper end of each ven-

tral merophyte is marked by a transverse band of four cells, indicating the place of attachment of an underleaf. Otherwise the merophyte is two cells wide, and it will be noted that the complete ventral merophyte figured is seven cells long on the left-hand side and eight cells long on the right-hand side. This indicates that the original peripheral cell of the very young merophyte (see Leitgeb, 1875, p. 5) undergoes one radial division and that this is followed by a series of three transverse divisions, the first giving rise to two cells in each row, the second to four, and the third (if complete) to eight. On the left-hand side of the merophyte figured one of the four cells formed by the second division failed to divide, so that only seven cells were formed. This seems to be the usual condition in the species under consideration.

The portion of the merophyte-boundary derived from the kathodic portion of the acroscopic wall extends from the group of four cells to the lobule on the left-hand side, and the portion derived from the anodic wall from the upper end of the lobule to the lower group of four cells. Similarly, the portion derived from the anodic portion of the acroscopic wall extends from the group of four cells to the lobule on the right-hand side, and the portion derived from the kathodic wall from the upper end of the lobule to the same group of cells. It will be seen at once that the portion derived from the kathodic portion of the acroscopic wall is much longer than that derived from the anodic portion and that the portion derived from the anodic wall is just as much shorter than that derived from the kathodic wall.

The conditions shown in figure 8, A, are illustrated diagrammatically in figure 8, G, which represents the surface of a stem rolled out to a plane. In this figure one series of lateral merophytes is repeated and two complete ventral merophytes, IV and VII, are shown. The same abbreviations are used as in figure 8, F, which represents segment IV prior to cell-division. It will be seen that *ack* in merophyte IV is longer than *acan* and that *an* is shorter than *k* by the same amount.

The free surfaces of the lateral merophytes in the leafy hepatics may deviate somewhat widely from the theoretical rectangular form. This is due in great part to the fact that the leaves are rarely transversely attached. If they are obliquely attached, as in species with distinctly incubous or succubous leaves, the free surface tends to be rhomboidal in form. This is clearly indicated in Buch's figure of *Cephalozia connivens* (1930, *f. 4, F*), in which the surfaces are shown to meet in a dorsal median line. The leaves in this species are succubous, and the upper end of each rhomboid, in consequence, forms an obtuse angle with the dorsal longitudinal side. If the leaves are complicate bilobed, as in *Radula* and the Lejeuneae,

another element of complexity is introduced. Leitgeb, fortunately, has given a careful description of the developing lateral merophytes in *Radula complanata,* and his account, in its more essential features, applies also to *Lejeunea flava.*

Each lateral segment in the *Radula,* according to Leitgeb's statements, divides in the usual way into two peripheral cells and an internal cell. The two peripheral cells bulge somewhat and the bulging portions represent the earliest rudiments of the lobe and lobule of the future leaf. As development proceeds the leaf-rudiment is cut off by walls, each of the two peripheral cells divides by a radial wall, and each of the four cells thus formed divides by a transverse wall. The cauline part of the young merophyte then consists of an acroscopic portion and a basiscopic portion, each composed of a transverse row of four cells (see Leitgeb, 1871, *pl. 12, f. 1, B* and *F*). The author goes on to show that the elongation of the merophyte takes place largely in the acroscopic portion, to which the leaf-rudiment is attached. During this process the line of attachment, which is slightly concave even at the beginning, becomes more sharply concave, and the mature lobe and lobule, in consequence, are almost longitudinally attached (1871, *pl. 11, f. 10 B*). Although Leitgeb does not indicate the boundaries of the mature lateral merophytes in *Radula complanata,* his description implies that their free surfaces meet in a dorsal median line and that the form of these surfaces is subrectangular.

In *Lejeunea flava* the presence of a dorsal row of cortical cells makes it evident that the free surfaces of the lateral merophytes do not meet in a median line. In other important respects, however, the merophytes agree with those of *Radula complanata.* The line of attachment of the leaves, for example, is essentially the same, as shown by figure 8, B, which represents the lateral view of a leaf-base. In this figure the two median rows of cells are lateral rows, the row on the left one of the ventral rows, and the row on the right the dorsal row. It will be seen that the line of attachment is strongly concave, that the lobe and lobule are almost longitudinally attached, and that four cells are present between the keel and the upper end of the lobe. These four cells indicate that the acroscopic portion of the young merophyte has taken part in the elongation of the stem, and that the original acroscopic cells have undergone a transverse division, followed by a second transverse division in each of the daughter-cells. But a comparison with figure 8, A, shows that four cells are present also in the lateral rows between the keels of the leaves and the lobules of the next older leaves on the same side. These four cells indicate that the basiscopic portion of the young merophyte has played an equally important part in the elongation of the stem, and that the original basiscopic cells have likewise under-

gone a series of two transverse divisions. It will be remembered that in *R. complanata* the predominant part in the elongation of the stem was played by the acroscopic portions of the young merophytes. Figure 8, B, shows further that the line of attachment of the lobe, throughout the greater part of its extent is on the outside of one of the lateral rows, whereas the line of attachment of the lobule is largely along the junction between the other lateral row and the adjoining ventral row. The same relationship is brought out in the cross-section of the stem of *L. flava*, shown in figure 6, L, as well as in some of the cross-sections of other species (see, for example, figure 6, H, left-side, and J).

An arrangement of the cortical cells in seven longitudinal rows, one of which is dorsal in position, is clearly shown by Leitgeb in two of his figures drawn from the northern *L. cavifolia* (Ehrh.) Lindb. (*L. serpyllifolia*), although he makes no mention of such an arrangement in his discussion of stem-structure in the leafy hepatics. These figures represent cross-sections, one (1875, *pl. 1, f. 1 B*) through a stem near the apical cell, the other (1875, *pl. 1, f. 8*) through the base of a young branch. Both figures show seven cortical cells, one of which is dorsal, but the first shows five medullary cells, whereas the second shows only three. The latter is essentially like the writer's figures of *Microlejeunea bullata* (fig. 6, N) and *Leptolejeunea elliptica* (fig. 6, P).

Although the writer has not studied the development of the merophytes in *L. flava*, it seems probable that the dorsal row of cortical cells is derived from both rows of lateral merophytes, a view first suggested by Dr. Hempstead Castle. If this view is correct each merophyte would pursue the normal course of development until the separation of the acroscopic portion from the basiscopic portion by means of transverse walls. At this stage each portion would have two peripheral cells side by side. The more dorsal cell in the acroscopic portion would then divide by a radial wall, but the corresponding cell in the basiscopic portion would undergo no such division. The succeeding transverse walls would divide each of the original cells into four cells, as already noted; and, as a result, the acroscopic portion of the merophyte would show three rows of cortical cells, each composed of four cells, whereas the basiscopic portion would show only two such rows. Since the cortical cells are approximately equal, and since the junction between the ventral side of a merophyte and the ventral merophytes is a straight line, as shown in figure 8, A, the extra row of cortical cells would necessarily project on the dorsal side. The extra rows in the lateral merophytes on the other side of the stem would project in the same way on the dorsal side and occupy the spaces between the projecting por-

tions of the merophytes on the first side. In this way the continuous dorsal row of cortical cells would be formed.

The conditions found in the stem of *Lejeunea flava* support the course of development just outlined. Figure 8, C, represents the upper surface of a stem from which the leaves have been dissected away and on which the boundaries of the merophytes are indicated by heavier lines. It will be seen that each merophyte shows four cells belonging to the dorsal row and eight cells to one of the lateral rows; the eight cells belonging to the other lateral row are not visible. At the upper end of each merophyte a small diamond-shaped cell at the junction of a leaf with the stem is indicated. The line of attachment of the lobe begins at the dorsal end of this cell, that is from about the middle of the dorsal row, extends along the upper end of the merophyte, and then downward along the side of the stem for a distance of four cells. The attachment of the lobe to a cell of the dorsal row is shown in figure 8, D, which represents the base of a lobe. It will be seen that the rounded basal cell with a papilla lies directly over the dorsal cell to which it is attached. The cell at the left of this rounded cell partially conceals the diamond-shaped cell described above. The fact that the leaves are attached to cells of the dorsal row is a further indication that this row is derived from lateral merophytes.

In the diagrammatic figure 8, E, it is shown that the kathodic portion of the acroscopic wall of one segment is the same as the kathodic wall of the first succeeding segment, and that the anodic portion is the same as the anodic wall of the second succeeding segment. In segment IV, for example, *ack* is the same as *k* in segment V, and *acan* the same as *an* in segment VI. The figure indicates further that *ack* of segment I forms an angle with *acan* of segment II, that the latter forms an angle with *ack* of segment IV, and so on. It follows from this that the kathodic and anodic portions of the acroscopic walls of the segments in two adjoining rows form a zigzag line extending from an angle of the diagram to the corresponding angle of the apical cell.

The diagrammatic figure 8, G, brings out the relationships, not only between the ventral and lateral merophytes but also between the two rows of lateral merophytes, so far as their free surfaces are concerned. The figure indicates also that the kathodic and anodic portions of the acroscopic walls of the lateral segments bend backward in the way described for the ventral segments. In this way the zigzag lines shown in figure 8, E, have become continuous longitudinal lines (see, in this connection Nägeli & Leitgeb, 1867, *p. 78, pl. 11, f. 3*) or, in the case of the zigzag line between the two rows of lateral segments, an alternating series of short longitudinal

lines, connected by shorter transverse lines. It may be further noted that in each lateral merophyte, just as in each ventral merophyte, *ack* is longer than *acan*.

Although the leaves and underleaves of *Lejeunea flava* and of most other leafy hepatics are arranged in a continuous spiral, the leaves are evenly spaced along the stem. In other words each leaf on one side of the stem is midway between two leaves on the opposite side. This signifies that the leaves and underleaves do not occur at equal intervals along the spiral, although the leaves themselves do so. If the spiral is dextrorse a complete half-turn of the spiral on the dorsal surface of the stem is taken up in passing from a leaf on one side to the next higher leaf on the other side, but the following half-turn on the ventral side would include an underleaf. It follows that the underleaf between two leaves in the spiral is closer to the leaves than these are to each other.

This relationship, also, is brought out by figure 8, G. It will be seen that the ventral merophyte IV is in contact with merophytes II and V on the left-hand side and with merophytes III and VI on the right-hand side, and that it is included between merophytes III and V in a ventral half-turn of the spiral. If it is assumed that the upper end of each merophyte, *acm*, indicates the line of attachment of a leaf or underleaf (or, in the case of the lateral merophytes, the upper limit of the line of attachment), *acan* in merophyte IV would represent the distance from the underleaf of that merophyte to the leaf of merophyte III and *acan* in merophyte V the distance from the same underleaf to the leaf of merophyte V. It will be seen that each of these distances is less than *acan* in merophyte III, which represents the distance between the leaf of merophyte III and the leaf of merophyte II. In fact *acan* in merophyte III is equal to *acan* in merophyte IV plus *acan* in merophyte V. The distribution of the leaves and underleaves at unequal intervals along the spiral represents a mechanism whereby the leaves are advantageously placed with reference to the rays of light.

It is safe to assume that the merophytes of the other Lejeuneae with seven rows of cortical cells are similar to those of *Lejeunea flava*. This is true, not only of species belonging to Schizostipae and Holostipae, but also of those belonging to the Paradoxae with underleaves, except that in the last group the ventral merophytes are only half as long as the lateral merophytes. The diagrammatic figure 8, G, therefore, would illustrate the condition found in these Paradoxae, if each ventral merophyte were divided by a median transverse line. In the still more simplified Paradoxae without underleaves the lateral merophytes clearly meet in a median longitudinal line on the dorsal surface of the stem, and this indicates that they are no broader in the acroscopic than in the basiscopic portion. The dia-

grammatic Fig. 8, H, based on *Aphanolejeunea microscopica*, represents the boundaries of the merophytes in such forms, and one row of lateral merophytes is repeated, just as in figure 8, G. It will be seen that the ventral merophytes are half the length of the lateral merophytes, that the latter are of the same width throughout, that each ventral merophyte is in contact with five other merophytes, and that each lateral merophyte is in contact with seven. It will be seen further that, although the acroscopic walls of the lateral segments have bent back on each side, the corresponding walls of the ventral segments have bent back on only one side.

No attempt has been made to map out the merophytes in Lejeuneae with more than seven rows of cortical cells. In the more complex forms belonging to this category, such as *Bryopteris filicina* (fig. 1) and *Ptychanthus striatus* (fig. 2), the cortical cells are in many rows and the rows are irregular, making it difficult to determine whether the lateral merophytes meet in a dorsal median line or not. But in some of the less complex forms, such as *Dicranolejeunea axillaris* (fig. 5, B) and *Odontolejeunea lunulata* (fig. 5, D), the rows of cortical cells are fewer and more regular, and a median dorsal row can be distinguished. It is evident that the lateral merophytes of such forms agree with those of *Lejeunea flava* in being broader in the acroscopic than in the basiscopic portion.

So far as the writer knows lateral merophytes of the type found in *L. flava* have not previously been recorded in the hepatics. Leitgeb, however, many years ago, described and figured similar merophytes in two mosses, *Fontinalis antipyretica* L. and *Sphagnum cuspidatum* Ehrh. In the *Fontinalis* (1868, *pl. 11, f. 7*) the acroscopic portion projects beyond the basiscopic on both sides; in the *Sphagnum* (1869, *pl. 8, f. 1*) on the anodic side only. The merophytes of the *Sphagnum* are thus similar to the lateral merophytes of *Lejeunea flava*, except that in the latter species the projecting portion of each merophyte is on the anodic side in one row of lateral merophytes and on the kathodic side in the other. This difference is clearly associated with the fact that the shoots of the *Lejeunea* are bilateral, whereas those of the *Sphagnum* are radial. The two rows of leaves in the *Lejeunea*, therefore, together with the merophytes of which they form parts, are symmetrically placed with respect to a vertical plane. The five rows of leaves in the *Sphagnum*, on the contrary, are arranged at equal intervals along a continuous spiral, without reference to any one longitudinal plane.

The boundaries of the merophytes inside the medulla may now be briefly considered. It has already been noted that these are theoretically in the form of longitudinal planes meeting in the axis of the stem and that they should appear in a cross-section as three converging lines. The cross-

section of *L. flava* (fig. 6, L) shows, however, that only zigzag lines are present, and that it is difficult to decide positively which of these zigzag lines represent the boundaries. In all probability the ventral group of four cells belongs to the ventral merophyte, the dorsilateral group of five cells on the right to the lateral merophyte showing three cortical cells (distinguishable by the attached lobe and lobule), and the dorsilateral group of four cells on the left to the lateral merophyte showing two cortical cells; but there is nothing except their position to distinguish the zigzag lines separating these groups of cells from other zigzag lines. In Lejeuneae with more complex medullae than that of *L. flava* the difficulties of distinguishing the boundaries are increased, as is evident from the cross-sections of such forms as *Taxilejeunea pterogonia* (fig. 6, B), *Neurolejeunea Breutelii* (fig. 3, C) and *Brachiolejeunea insularis* (fig. 5, A). It is only in the highly simplified species with but three rows of medullary cells, such as *Microlejeunea bullata* (fig. 6, N) and *Diplasiolejeunea unidentata* (fig. 7, B), that the boundaries between the merophytes in the medulla are actually straight lines. Here there is no question that each row of merophytes has a single row of medullary cells. The fact that the still more simplified Paradoxae without underleaves have only one row of medullary cells would seem to indicate that the ventral segments in these forms were the only ones that cut off internal cells. In accordance with this idea each merophyte in such a stem as that of *Aphanolejeunea microscopica* (fig. 7, F) would be composed of only two rows of cells, the ventral merophyte of one medullary and one cortical row, and each lateral merophyte of two cortical rows.

MATERIAL EXAMINED

The stem-structure of thirty-five species of the Lejeuneae, representing twenty-nine genera, is discussed in the preceding pages. The descriptions and figures of these various species have been drawn from the following specimens: *Anoplolejeunea conferta*, near the Finca Sepacuite, Guatemala, *O. F. Cook and R. F. Griggs*, 1902, No. 190; *Aphanolejeunea microscopica*, Ballachulich, Argyllshire, Scotland, *S. M. Macvicar*, 1904; *Archilejeunea Spruceana*, near Bartica, British Guiana, *P. W. Richards*, 1929, No. 201; *Brachiolejeunea insularis*, near Castleton Botanical Garden, Jamaica, *L. M. Underwood*, 1903, No. 55; *Bryopteris filicina*, Old England Falls, Jamaica, *L. M. Underwood*, 1903, No. XX; *Caudalejeunea Lehmanniana*, Hattie Bauer Hammock, Florida, *J. K. Small and C. A. Mosier*, 1915, No. 5301; *Colura ornata*, Mt. Salak, Java, *V. Schiffner*, 1893, distributed in Fr. Verdoorn, Hep. Select. et Crit., No. 151; *Cyclolejeunea chitonia*, El Yunque, Porto Rico, *A. W. Evans*, 1902, No. 82; *C. convexistipa*, Mora Forest, east of Sangre Grande, Trinidad, *E. G. Britton*, No. 2871a; *C. peruviana*,

Aripo Savanna, Trinidad, *R. Thaxter*, 1913; *Cystolejeunea lineata*, El Yunque, Porto Rico, *A. W. Evans*, 1902, No. 46 in part; *Dicranolejeunea axillaris*, Ecuador, *R. Spruce*, distributed in Hep. Spruceanae; *Diplasiolejeunea pellucida*, John Crow Peak, Jamaica, *A. W. Evans*, 1903, No.135 in part; *D. unidentata*, Mansfield, near Bath, Jamaica, *A. W. Evans*, 1903, No. 336; *Drepanolejeunea inchoata*, El Yunque, Porto Rico, *A. W. Evans*, 1902, No. 117; *Euosmolejeunea trifaria*, Mansfield, near Bath, Jamaica, *A. W. Evans*, 1903, No. 341; *Hygrolejeunea cerina*, Banao Hills, Santa Clara, Cuba, *Brother Clement*, 1915, No. 25; *Lejeunea flava*, Chinchona, Jamaica, *A. W. Evans*, 1906, No. 409; *L. inundata*, near Bartica, British Guiana, *P. W. Richards*, 1929, No. 365; *Leptocolea planifolia*, Utuado, Porto Rico, *M. A. Howe*, 1906, No. 862 in part; *L. scabriflora*, Sulphur River, Bath, Jamaica, *A. W. Evans*, 1903, No. 322b; *Leptolejeunea elliptica*, Green River Valley, Jamaica, *A. W. Evans*, 1903, No. 212 in part; *Leucolejeunea xanthocarpa*, Indefatigable Island, Galapagos Islands, *J. T. Howell*, 1932, No. 257 in part; *Mastigolejeunea auriculata*, Eustis, Florida, *L. M. Underwood*, 1891, No. 84; *Microlejeunea bullata*, Sanford, Florida, *S. Rapp*, 1913, No. 78; *Neurolejeunea Breutelii*, trail to Vinegar Hill, Jamaica, *A. W. Evans*, 1906, No. 453, distributed in C. C. Haynes, Amer. Hep. No. 65; *Odontolejeunea lunulata*, near Bartica, British Guiana, *P. W. Richards*, 1929, No. 492; *Omphalanthus filiformis*, near Hardware Gap, Jamaica, *A. W. Evans*, 1903, No. 183; *Potamolejeunea orinocensis* Steph., near Bartica, British Guiana, 1929, *P. W. Richards*, No. 367; *Ptychanthus striatus*, Mt. Singalang, Sumatra, *V. Schiffner*, 1894, distributed in Fr. Verdoorn, Hep. Select. et Crit., No. 264; *Pycnolejeunea macroloba*, near Bartica, British Guiana, *P. W. Richards*, 1929, No 443a; *Stictolejeunea Kunzeana*, Chimborazo, Ecuador, *R. Spruce*, distributed in Hep. Spruceanae; *S. squamata*, Troy, Jamaica, *A. W. Evans*, 1906, No. 678; *Taxilejeunea pterogonia*, San Miguel, Urubamba Valley, Peru, *O. F. Cook and G. B. Gilbert*, 1915, No. 1180; *Thysananthus amazonicus*, near Bartica, British Guiana, *P. W. Richards*, 1929, No. 188.

SUMMARY

The stems of the Lejeuneae show a differentiation into a medulla and a unistratose cortex, the cells of which are arranged in more or less distinct longitudinal rows.

The medullary cells, with few exceptions, are more than twice the length of the cortical cells but have a smaller diameter.

The stems of the Holostipae, as a rule, are more complexly organized than those of the Schizostipae and Paradoxae, and the last named group includes the most simply organized stems of all.

The highest degree of differentiation is found in the horizontally spreading secondary stems of certain Holostipae, in which a distinct skeletal tissue composed of fiber-like cells is developed at the periphery of the medulla.

In stems of this character the medulla is sixteen to twenty cells thick from top to bottom, and the number of rows of cortical cells may be as high as seventy.

In passing from the more complex Holostipae to the less complex the rows of cortical cells become fewer and fewer, reaching a limit of seven rows in a few cases.

In the Schizostipae, with few exceptions, the cortical cells are definitely in seven longitudinal rows, one of which is dorsal in position, two on each side lateral, and two ventral.

In the Paradoxae with underleaves the cortical cells have the same arrangement as in the majority of the Schizostipae; in the Paradoxae without underleaves, however, the cortical cells are in only five or six rows, two of which on each side are lateral in position and the remaining one or two ventral.

In passing from the most complex Holostipae to the simplest Paradoxae the medulla becomes more and more reduced, reaching a limit in the Paradoxae without underleaves, in which only one row of medullary cells is present.

From the standpoint of evolution the more primitive types of stems in the Lejeuneae are apparently those found in certain Holostipae.

From stems of this character two lines of advance may perhaps be recognized, one leading to greater complexity and the other to simplification and reduction, culminating in the Paradoxae without underleaves.

The cortical cells in the stems of the Lejeuneae, especially if their cavities are large, may play a part in the storage of water, as well as in the processes of absorption and photosynthesis.

Thick cell-walls in either cortex or medulla form a part of the skeletal system of the plant but may be even more important on account of their power of imbibing water rapidly.

The adult shoot in the Lejeuneae is made up of two rows of lateral merophytes and one row of ventral merophytes, each merophyte being derived from one of the segments cut off from the apical cell.

Each merophyte consists of a leaf or underleaf and of a portion of the stem, which is theoretically in the form of a sector of a cylinder.

In the more complex types of stem, with numerous rows of cortical cells, the superficial boundaries of the merophytes are indistinct; but in

stems with seven rows of cortical cells, or fewer, the superficial boundaries are more definite.

In *Lejeunea flava*, which may be considered typical of forms with seven rows, the ventral merophytes are two cells in width by about eight cells in length and are separated from the lateral merophytes by approximately straight lines.

The lateral merophytes, however, which are also about eight cells long, are three cells wide in the upper half and only two cells wide in the lower half.

The extra rows in the upper halves of successive merophytes are continuous with one another and form the dorsal row of cortical cells, which is therefore derived from both rows of lateral segments.

The rows of lateral merophytes, in consequence, instead of being separated from one another by a straight line, are separated by a series of short longitudinal lines of equal length connected by shorter transverse lines.

In the Paradoxae without underleaves, typified by *Aphanolejeunea microscopica*, the lateral merophytes are two cells wide throughout and are separated from one another by a straight line.

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The Oedogoniaceae of Oklahoma including new species and varieties[1]

CLARENCE E. TAFT

(WITH PLATES 15 AND 16)

During the past two years the writer has carried on a survey of the algae of Oklahoma based on approximately four hundred collections made during the spring of 1932 and the summer of 1933. As a partial result of this survey, sixty-four species and varieties of the two genera, *Bulbochaete* and *Oedogonium*, have been recorded. Of this number ten are new to science, while one formerly regarded as a form has been given varietal rank, and two others have been returned to varietal rank. Exclusive of those newly described, six are new records for the United States and are indicated as such by an asterisk. In addition, critical notes have been added wherever the material differed enough to justify such an addition.

With but one exception, that of *Oe. exocostatum* which appeared in the late summer, all species listed were found in fruiting condition in collections dating from May 1 to May 15, 1932.

Although the collections were representative of the entire state, the range of distribution of these two genera is quite limited, coinciding closely with the shale and sandstone mountain areas along the eastern border. While present in small numbers they never formed a conspicuous group in the prairie regions, a fact which also was true of the granite and limestone mountains in the southwestern part of the state.

The genus *Oedocladium* has not been recorded from Oklahoma.

Acknowledgement is due Dr. L. H. Tiffany of the Department of Botany of this University for his kindness in checking the new species, and for his helpful suggestions and criticisms throughout the preparation of the report. Also to Mrs. Taft, through whose efforts the spore drawings were made possible.

BULBOCHAETE Agardh.

1. **B. alpina** sp. nov. (figs. 5 and 6).

B. dioica, nannandria, idioandrospora; oogoniis depresso-globosis, pantentibus, sub setis terminalibus setis; oosporis eadem forma ac oogoniis, mesosporio scrobiculis angulare ornato, seriebus scrobiculorum; dissepimento cellularum suffultoriarum fere mediano; androsporangiis epigynis, 1–3 cellularibus; nannandribus in oogoniis sedentibus, antheridio exteriore, stipite curvato, unicellulari; cell. veget. 20–30$\times$53–106μ; oogon. 59$\times$53–56μ; oospor. 58$\times$51–54μ; cell. androsp. 17–20$\times$13–17μ; stip. nannandr. 10–11$\times$36–46μ; cell. antherid. 10–11$\times$15–17μ.

[1] Contributions from Department of Botany, Ohio State Univ. No. 343.

Dioecious, nannandrous, idioandrosporous, oogonium depressed globose, patent, below the terminal setae; oospore of the same form as the oogonium, middle spore wall scrobiculate, pits angular, concentrically arranged; division of the suffultory cell median; androsporangium 1–3, epigynous; dwarf male on the oogonium, curved, antheridium 1, exterior; vegetative cell 20–30×53–106μ; oogonium 59×53–56μ; oospore 58×51–54μ; androsporangium 17–20×13–17μ; dwarf male stripe 10–11×36–46μ; antheridium 10–11×15–17μ.

Herb. C.E.T. 310.

This species is characterized by a scrobiculate oospore in which the pits are angular. In size it is to be compared to *B. gigantea*.

2. **B. areolata** sp. nov. (figs. 7 and 8).

B. dioica, nannandria, gynandrospora; oogoniis ellipsoideis, patentibus vel erectis, sub androsporangiis vel setis terminalibus vel sub cellulis vegetativis, androsporangiis feris setis; oosporis ellipsoideis, episporio oosporae profunde areolato (in sectione optica profunde undulato); dissepimento cellularum suffultoriarum supremus; androsporangiis 4-cellulariabus, epigynis; nannandribus paullum curvatis, in cellulis vegetativis sedentibus, antheridio exteriore, 1–3 cellulari; cell. veget. 15–20×20–46μ; oogon. 33–36×53–63μ; oospor. 31–35×52–59μ; cell. androsp. 20–26×17–23μ; stip. nannandr. 13–15×23–25μ; cell. antherid. 7–10×4–7μ.

Dioecious, nannandrous, gynandrosporous; oogonium ellipsoid, patent to erect, below the androsporangia, terminal setae, or vegetative cells; oospore ellipsoid, outer spore wall deeply areolate with sharp points at the angles of the areolations (in section deeply undulate); division of the suffultory cell supreme; androsporangium 1–4, epigynous; dwarf male slightly curved, on the vegetative cells, antheridium 1–3, exterior.

Vegetative cell 15–20×20–46μ; oogonium 33–36×53–63μ; oospore 31–35×52–59μ; androsporangium 20–26×17–23μ; dwarf male stipe 13–15×23–25μ; antheridium 7–10×4–7μ.

Herb. C.E.T. 312.

This species is characterized by the deeply areolate outer spore wall, a type of spore marking which is not found anywhere else in the genus *Bulbochaete*.

3. *B. crassiuscula* Nordst.

4. *B. crenulata* Pringsheim

5. **B. cimarronea** sp. nov. (figs. 1 and 2).

B. dioica, nannandria, gynandrospora; oogoniis ellipsoideis, patentibus, sub setis terminalibus vel rarissime sub cellulis vegetativis setis; oosporis ellipsoideis, costis episporii oosporarum, ut videtur, glabris, non crenatis; dissepimento cellularum suffultoriarum supremus; androsporangiis epigynis, 1–2 cellularibus; nannandribus in cellulis vegetativis, raro in oogoniis ipsis sedentibus, antheridio exteriore, 1–2 cellulari; cell. veget. 14–17×17–23μ;

oogon. 26–29×36–39μ; oospor. 24–26×35–37μ; cell. androsp. 10–11×5–7μ; stip. nannandr. 13–17×20–23μ; cell. antherid. 7–8×5–7μ.

Dioecious, nannandrous, gynandrosporous, oogonium ellipsoid, patent, below the terminal setae or rarely below the vegetative cells; oospore ellipsoid, outer spore wall longitudinally ribbed, ribs entire; division of the suffultory cell supreme; androsporangium 1–2, epigynous, dwarf male located on vegetative cell, rarely on the oogonium, antheridium 1–2, exterior; vegetative cell 14–17×17–23μ; oogonium 26–29×36–39μ; oospore 24–26×35–37μ; androsporangium 10–11×5–7μ; dwarf male stipe 13–17×20–23μ; antheridium 7–8 ×5–7μ.

Herb. C.E.T. 163.

This species is among the smallest known forms combining the characters of the ellipsoid oogonium and longitudinally ribbed, ellipsoid spore. It is to be compared with *B. pygmaea* from which it differs by the presence of a divided suffultory cell, and the entire ridges of the oospore.

6. **B. Furberae** Collins **var. depressa** var. nov. (figs. 3 and 4).

Ogoniis sub setis terminalibus vel rarius sub cellulis suffultoris setis; androsporangiis 1–3 cellularibus, epigynis; nannandribus in oogoniis vel prope ea sedentibus, antheridio interiore, stipite paullum curvato; cell. veget. 13–17× 33–83μ; oogon. 46–50×35–37μ; oospor. 44–48×32–35μ; cell. androsp. 11–14 ×6–10μ; nannandr. 10–12×26–30μ. Certerum ut in typo.

Oogonium terminal (rarely below the suffultory cell); androsporangium 1–3, epigynous; dwarf males curved, on or near the oogonia, antheridium interior; vegetative cell 13–17×33–83μ; oogonium 46–50×35–37μ; oospore 44–48×32–35μ; androsporangium 11–14×6–10μ; dwarf male 10–12×26–30μ.

Herb. C.E.T. 312.

This variety differs from the type in the larger size of the reproductive structures. It should be compared to *B. brebissonii* in which the division of the suffultory cell is basal.

7. *B. gigantea* Pringsheim

8. *B. intermedia* De Bary

*9. *B. minuta* West and West

*10. *B. nana* Wittr.

Oogonia and oospores slightly broader and longer; oogonium 26–30 ×36–42μ; oospore 25–28×35–41μ.

11. *B. Nordstedtii* Wittr.

12. *B. obliqua* Lundell

The oogonia and oospores were narrower than in the type; oogonium 50–53×43–46μ; oospore 49–51×42–45μ.

13. *B. rectangularis* Wittr.

14. *B. rectangularis* Wittr. var. *hiloensis* Nordst.

Vegetative cell 16–20×26–33μ; oogonium 29–33×43–49μ; oospore 26–30×38–45μ; androsporangium 13–17×13–15μ; dwarf male stipe 13–17 ×23–27μ; antheridium 8–9×5–7μ.

The original dimensions of this variety have been rewritten so as to include the slight variations of the Oklahoma material.

15. *B. repanda* Wittr.

OEDOGONIUM Link

1. *Oe. armigerum* Hirn

Vegetative cell 9–13×36–100μ; oogonium 29–33×30–35μ; oospore 26–30×26–29μ; dwarf male, lower cell 7–8×20–24μ, upper cell 4–6×21–30μ; antheridium 5–6×7–8μ.

This description combines the original dimensions with those of the Oklahoma material.

2. *Oe. aster* Wittr.

Vegetative cell 7–13×50–110μ; oogonium 33–37×(27–)30–39μ; oospore 29–32×25–30μ; dwarf male stipe 6–7×20–25μ; antheridium 5–6×7–8μ.

These are the original dimensions combined with those of the Oklahoma material.

3. *Oe. bohemicum* Hirn

4. *Oe. borisianum* (Le Cl.) Wittr.

5. *Oe. Boscii* (Le Cl.) Wittr. var. *occidentale* Hirn

Vegetative cell 8–16×50–165μ; oogonium 29–38×69–100μ; oospore 29–37×42–50μ; antheridium 12–13×10–16μ.

These are a combination of the original and the Oklahoma dimensions.

6. *Oe. Braunii* Kuetz.

7. *Oe. capitellatum* Wittr.

8. *Oe. cardiacum* (Hass.) Wittr.

9. *Oe. cardiacum* (Hass.) Wittr. var. *carbonicum* Wittr.

In this variety the oospore was smaller, being 36–40×39–43μ instead of 40–52×46–65μ.

10. *Oe. cardiacum* (Hass.) Wittr. var. *minus* Lemmerman

The oogonium and oospore were slightly larger. Oogonium 46–50×43–59μ; oospore 40–43×40–42μ.

11. *Oe. concatenatum* (Hass.) Wittr.

12. **Oe. concatenatum** (Hass.) Wittr. **var. regulare** var. nov. (fig. 20).

Oogoniis singulis, suboviformibus vel quadrangulari ellipsoidies; oosporiis eadem forma ac oogoniis, mesosporio scrobiculato, seriebus scrobiculorum; cell. veget. 23–26×89–142μ; cell. suffult. 53–59×105μ; oogon. 66–69×99–106μ; oospor. 63–68×83–86μ; cell. androsp. 32×32μ; stip. nannandr. 16–20 ×57–70μ; cell. antherid. 12–15×8–16μ. Certerum ut in typo.

Oogonium single, subovoid to quadrangularly-ellipsoid; oospore of the same form as the oogonium, median spore wall scrobiculate, scrobiculations concentrically arranged. Vegetative cell 23–26×89–142μ; suffultory cell 53–59 ×105μ; oogonium 66–69×99–106μ; oospore 63–68×83–86μ androsporangium 32×32μ; dwarf male stipe 16–20×57–70μ; antheridium 12–15×8–16μ.

Herb. C.E.T. 196.

In *Oe. concatenatum* the pits of the median spore wall are arranged in longitudinal series, while in this variety they are arranged concentrically. Furthermore the subovoid to quadrangularly-ellipsoid spore readily separates it from the variety *hutchensiae* (Wittr.) Hirn whose spores are nearly globose.

13. *Oe. crassiusculum* Wittr.

14. *Oe. crassiusculum* Wittr. var. *arechavaletae* (Wittr.) Hirn

The diameter of the vegetative cells of the Oklahoma material was greater than that of the type. Vegetative cell 33–35×66–108μ. This variety is idioandrosporous.

15. *Oe. crassiusculum* Wittr. var. *cataractum* (Wolle) Tiffany

16. *Oe. crassiusculum* Wittr. var. *idioandrosporum* Nordst. and Wittr.

17. *Oe. crassum* (Hass.) Wittr.

18. *Oe. crispum* (Hass.) Wittr.

19. *Oe. crispum* (Hass.) Wittr. var. *gracilescens* Wittr.

20. *Oe. crispum* (Hass.) Wittr. var. *granulosum* Nordst.

[*Oe. crispum* (Hass.) Wittr. f. *granulosum* (Nordst.) Hirn]

Oogonium subglobose to obovoid-globose, almost completely filled by the oospore; antheridium subepigynous or hypogynous; wall of oospore punctate-granulate; vegetative cell 13–17×29–63μ; oogonium 36–43×42–46μ; oospore 34–40×34–40μ; antheridium 8–13×7–11μ. Otherwise as in the type.

Herb. C.E.T. 56.

21. *Oe. cryptoporum* Wittr.

22. *Oe. cryptoporum* Wittr. var. *vulgare* Wittr.

23. *Oe. cyathigerum* Wittr.

24. *Oe. cyathigerum* Wittr. var. *ellipticum* Magnus and Wille

Gynandrosporous; vegetative cell 19–30×30–132μ; suffultory cell 26–46 ×40–125μ; oogonium 50–66×(59–) 68–94μ; oospore 48–65×45–66 (–73)μ; androsporangium 1–6, 23–26×14–19μ; dwarf male stipe 13–18×43–59μ.

These dimensions combine the original with those of the Oklahoma material. The androsporangia are described for the first time.

25. *Oe. echinospermum* Al. Br.

26. *Oe. exocostatum* Tiffany

27. **Oe. flavescens** (Hass.) Wittr. **var. minus** var. nov. (figs. 10, 11, 12).

Idioandrosporum; poro mediano vel infra medium apertis; oosporiis globosis vel sub-globosis; androsporangiis 1–3 cellularibus; antheridio exteriore, uni-cellulari; cell. veget. 16–20×62–112μ; oogon. 39–46×46–50μ; oospor. 36–43×36–43μ; cell. androsp. 16–23×10–20μ; stip. nannandr. 10–13×33–45μ; cell. antherid. 8–10×7–13μ. Certerum ut in typo.

Idioandrosporous; pore median to inframedian; oospore globose to subglobose; androsporangium 1–3; antheridium 1, exterior; vegetative cell 16–20×62–112μ; oogonium 49–46×46–50μ; oospore 36–43×36–43μ; androsporangium 16–23×10–20μ; dwarf male stipe 10–13×33–45μ; antheridium 8–10×7–13μ.

Herb. C.E.T. 53.

The variety *minus* closely resembles the type except in its smaller size. This along with the inframedian position of the pore and the subglobose oospore, both of which are commonly present, give this form varietal rank.

28. **Oe. fuscum** sp. nov. (figs. 13, 14 and 15).

Oe. dioicum, nannandrium, gynandrosporum; oogoniis singulis, ellipsoideis vel ellipsoideo-globosis vel globosis, poro mediano vel infra medium apertis; oosporiis ellipsoideo-globosis vel globosis; oogoniis complentibus vel non complentibus; episporio reticulato-verrucoso, fusco; cellulis suffultoriis tumidis; androsporangiis ?–3 cellularibus, epigynis; nannandribus paullum curvatis, in cellulis suffultoriis sedentibus, antheridio exteriore, 1–2 cellulari; cell. veget. 10–17×33–73μ; cell. suffult. 23–27×50–53μ; oogon. 36–43×46–56μ; oospor. 34–40×42–46μ; cell. androsp. 10–11×7–10μ; stip. nannandr. 7–9×20–23μ; cell. antherid. 6–7×5–7μ.

Dioecious, nannandrous, gynandrosporous, oogonium single, ellipsoid to ellipsoid-globose to globose, pore median to inframedian; oospore ellipsoid-globose to globose, completely filling or not completely filling the oogonium; outer spore wall reticulate-verrucose, brown; suffultory cell enlarged; androsporangium ?–3, epigynous; dwarf male slightly curved, on suffultory cell, antheridium 1–2, exterior; vegetative cell 10–17×33–73μ; suffultory cell 23–27×50–53μ; oogonium 36–43×46–56μ; oospore 34–40×42–46μ; androsporangium 10–11×7–10μ; dwarf male stipe 7–9×20–23μ; antheridium 6–7×5–7μ.

Herb. C.E.T. 305.

Due to the reticulate-verrucose outer spore wall, this species occupies a unique position in the genus *Oedogonium*, and may be readily separated from all the known species by this one character.

29. *Oe. giganteum* Kuetz.; Wittr.

The diameter of the vegetative cells of this species was slightly greater, being 49–53μ instead of 30–50μ.

30. *Oe. grande* Kuetz.; Wittr.

31. *Oe. grande* Kuetz.; Wittr. var. *angustum* Hirn

32. *Oe. Gunnii* Wittr.

*33. *Oe. Howardii* G. S. West

Vegetative cell 9–13×23–43μ; oogonium 26–31×23-30μ; oospore 20–27×20–27μ.

Part of the Oklahoma material was typical of *Oe. Howardii*, while in the same collections some filaments had smaller oogonia and oospores. Based on this material as well as that from Puerto Rico recently examined by Dr. L. H. Tiffany, *Oe. Howardii* and its variety *minus* are not easily separable.

34. **Oe. illinoisense** Transeau **var. oklahomense** var. nov. (figs. 24–26).

(?) Idioandrosporum; costis spiralibus numero 4–6, non utrinque in polo; cellula fili basali forma, ut vulgo, elongata; (?) androsporangiis; antheridio exteriore unicellulari; cell. veget. 10–20×73–125μ; cell. suffult. 26–34×69–75μ; oogon. 49–56×60–65μ; oospor. 43–46×43–46μ; stip. nannandr. 11–13×38–46μ; cell. antherid. 7–9×12–13μ. Certerum ut in typo.

(?) Idioandrosporous; outer spore wall with 4–6 spiral ribs, not united at the poles; basal cell elongate; (?) androsporangium; antheridium 1, exterior; vegetative cell 10–20×73–125μ; suffultory cell 26–34×69–75μ; oogonium 49–56×60–65μ; oospore 43–46×43–46μ; dwarf male stipe 11–13×38–46μ; antheridium 7–9×12–13μ.

Herb. C.E.T. 240.

In general appearance this variety resembles the species, but differs in its smaller size and by not having the spiral ribs united at the poles.

35. *Oe. intermedium* Wittr.

36. *Oe. irregulare* Wittr.

37. *Oe. irregulare* Wittr. var. *condensatum* (Hallas) Hirn

38. *Oe. Landsboroughi* (Hass.) Wittr.

*39. *Oe. longicolle* Nordst. var. *senegalense* Nordst.

40. *Oe. macrandrium* Wittr. var. *aemulans* Hirn

[*Oe. macrandrium* Wittr. f. *aemulans* Hirn]

Vegetative cell 10–16×22–90μ; oogonium 28–42×33–45(–50)μ; oospore 26–36×26–36μ; dwarf male stipe 9–12×20–25μ; antheridium 6–9×7–10μ. Otherwise as in type.

Herb. C.E.T. 56.

This variety is characterized by the narrow vegetative cells and globose oospore. It differs from the form *lundense* by its longer vegetative cells.

41. *Oe. macrandrium* Wittr. var. *Hohenackerii* (Wittr.) Tiffany

42. *Oe. macrandrium* Wittr. var. *propinquum* (Wittr.) Hirn

43. *Oe. mexicanum* Wittr.

44. *Oe. mitratum* Hirn

45. *Oe. multisporum* Wood
46. *Oe. nebraskense* Ohashi
47. **Oe. oblongum** Wittr. **var. sphaericum** (Hallas) comb. nov. (fig. 21).

[*Oe. sphaericum* Hallas; *Oe. oblongum* Wittr. f. *sphaericum* (Hallas) Hirn]

Oospore globose to globose-ovoid; oogonium not completely filled by the oospore; vegetative cell 5–11×20–86μ; oogonium 21–28×30–52μ; oospore 16–27×16–30μ; antheridium 8–9×6–7μ. Otherwise as in type.

Herb. C.E.T. 232.

Hirn (1906) relegated *Oe. sphaericum* Hallas to *Oe. oblongum* Wittr. forma *sphaericum* (Hallas). Because of the appearance in the Oklahoma collections of material which extends the original description, but which undoubtedly belongs to this form, it has been given varietal rank.

*48. *Oe. oboviforme* Wittr.

This form had a slightly smaller oogonium; oogonium 59–63×76–99μ.

49. **Oe. ouchitanum** sp. nov. (figs. 22 and 23).

Oe. monocium, oogoniis singulis vel 2 continuis, pyriformibus vel subpyriformibus, operculo apertis, circumscissione superiore; oosporiis globosis (raro subglobosis), partem inferiorem vel submedianem, inflatam oogoniorum complentibus, membrana laevi; antheridiis ?–3, sparis, cellulis vegetativis capitellatis; cellula fili basali forma, ut vulgo, elongata; cellula fili terminali obtusa; cell. veget. 5–13×33–50μ; oogon. 30–33×33–40μ; oospor. 26–30×23–30μ; cell. antherid. 8–9×10–13μ.

Monoecious, oogonium 1–2, pyriform to subpyriform, opening by a superior operculum; oospore globose (rarely subglobose), not filling the oogonium longitudinally, wall smooth; antheridium ?–3, scattered; vegetative cell capitellate; basal cell elongate; terminal cell obtuse; vegetative cell 5–13×33–50μ; oogonium 30–33×33–40μ; oospore 26–30×23–30μ; antheridium 8–9×10–13μ.

Herb. C.E.T. 305.

The combination of capitellate vegetative cells and pyriform oogonia is the distinguishing character of this species, in that it is the only species in which the two are combined. It is to be compared with *Oe. simplex* and *Oe. pyrulum*, both of which have cylindrical vegetative cells, and with *Oe. pyriforme* and *Oe. pithophorae* which have cylindrical vegetative cells as well as different dimensions.

50. *Oe. paludosum* (Hass.) Wittr. var. *parvisporum* Hirn
51. *Oe. paucocostatum* Transeau
52. *Oe. plagiostomum* Wittr. var. *gracilius* Wittr.
53. *Oe. princeps* (Hass.) Wittr.
54. *Oe. Pringsheimii* Cramer; Wittr. var. *abbreviatum* Hirn (fig. 9)

Dioecious; vegetative cell 10–16×15–39μ; oogonium 28–33×29–36μ; oospore 27–30×27–30μ; antheridium 1-4, division horizontal, 9–14×5–10μ.

These dimensions combine the variations of the Oklahoma material with those of the original descriptions. The antheridia, heretofore unknown, are described and figured.

55. *Oe. pungens* Hirn

The length of the vegetative cells was 66-128μ. This exceeds the length given in the original description by 34μ.

56. *Oe. pusillum* Kirchner

*57. *Oe. rigidium* Hirn

Vegetative cell 14–16×38–54μ; oogonium 40–43×35–48μ; oospore 32–35×32–35μ. The oogonia are longer than in the type.

58. *Oe. Rothii* (Le Clerc) Pringsheim

59. *Oe. rufescens* Wittr. var. *exiguum* (Elfv.) Tiffany

60. *Oe. rugulosum* Nordst. var. *minutum* (Hansgirg) Hirn

61. *Oe. Sancti Thomae* Wittr. and Cleve

62. *Oe. suecicum* Wittr. var. *australe* (G.S.West) B.H.Smith

63. **Oe. subglobosum** sp. nov. (figs. 16–19).

Oe. dioicum, nannandrium, (?) idioandrosporum; oogoniis 2–10 continuis (raro singulis), globosis vel subglobosis, operculo apertis, circumscissione superiore; oosporiis subglobosis, oogonia fere complentibus, membrana laevi; cellulis vegetativis capitellatis; cellulis suffultoriis non vel paullulum tumidis; cellula fili basali forma, ut vulgo, elongata; nannandribus paullum curvatis, in oogoniis sedentibus, antheridio exteriore, uni-vel bicellulari; cell. veget. 13–20×49–83μ; cell. suffult. 23–33×39–43μ; oogon. 43–50×40–50μ; oospor. 40–46×36–40μ; stip. nannandr. 10–13×23–33μ; cell. antherid. 6–10×4–7μ.

Dioecious, nannandrous, (?) idioandrosporous; oogonium 1–10 (rarely single), globose to subglobose, superior operculum; oospore subglobose, quite filling the oogonium, spore wall smooth; vegetative cells capitellate; suffultory cell sometimes enlarged; basal cell elongate; dwarf male slightly curved, on the oogonium; antheridium 1–2, exterior. Vegetative cell 13–20×49–83μ; suffultory cell 23–33×39–43μ; oogonium 43–50×40–50μ; oospore 40–46×36–40μ; dwarf male stipe 10–13×23–33μ; antheridium 6–10×4–7μ.

Herb. C.E.T. 309.

This species together with *Oe. rigidium* are the only nannandrous species having the combination of superior position of the oogonial operculum, and capitellate vegetative cells. It is distinguished from the latter by the series of oogonia (1-10), subglobose oospore, and the larger size.

64. *Oe. tapeinosporum* Wittr.

The following is a summary of the new species and varieties named:

Bulbochaete alpina, *B. areolata*, *B. cimarronea*, *B. Furberae* Collins var. *depressa*, *Oedogonium concatenatum* (Hass.) Wittr. var. *regulare*, *Oe. flavescens* (Hass.) Wittr. var. *minus*, *Oe. illinoisense* Transeau var. *olkahomense*, *Oe. oblongum* Wittr. var. *sphaericum* (Hallas), *Oe. ouchitanum*, *Oe. subglobosum*, *Oe. fuscum*.

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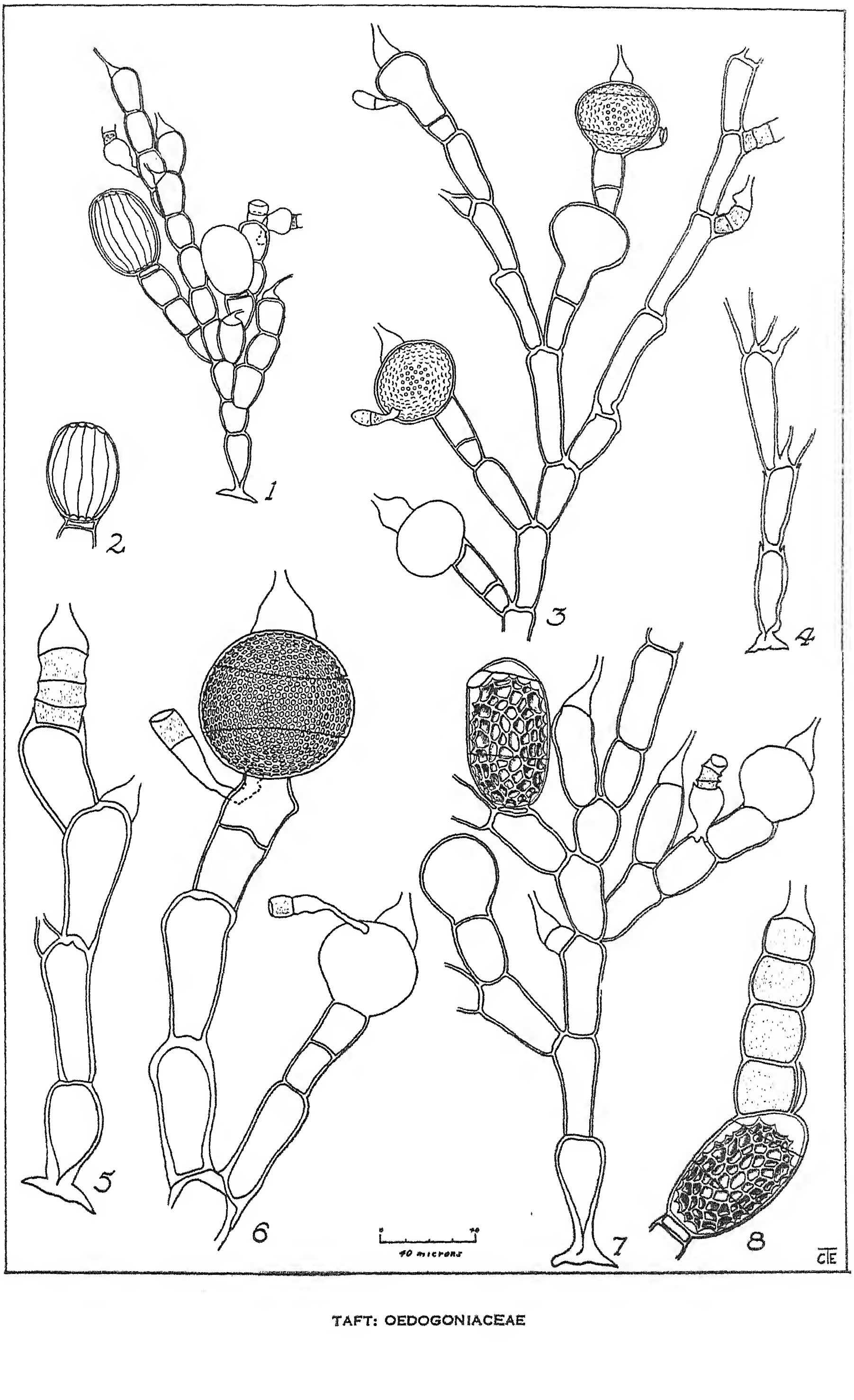
Explanation of plate 15

Figs. 1 and 2. *Bulbochaete cimarronea* Taft
Figs. 3 and 4. *B. Furberae* Collins var. *depressa* Taft
Figs. 5 and 6. *B. alpina* Taft
Figs. 7 and 8. *B. areolata* Taft

Explanation of plate 16

Fig. 9. *Oedogonium Pringsheimii* Cramer; Wittr. var. *abbreviatum* Hirn
Figs. 10–12. *Oe. flavescens* (Hass.) Wittr. var. *minus* Taft
Figs. 13–15. *Oe. fuscum* Taft
Figs. 16–19. *Oe. subglobosum* Taft
Fig. 20. *Oe. concatenatum* (Hass.) Wittr. var. *regulare* Taft
Fig. 21. *Oe. oblongum* Wittr. var. *sphaericum* (Hallas) Taft
Figs. 22 and 23. *Oe. ouchitanum* Taft
Figs. 24–26. *Oe. illinoisense* Transeau var. *oklahomense* Taft



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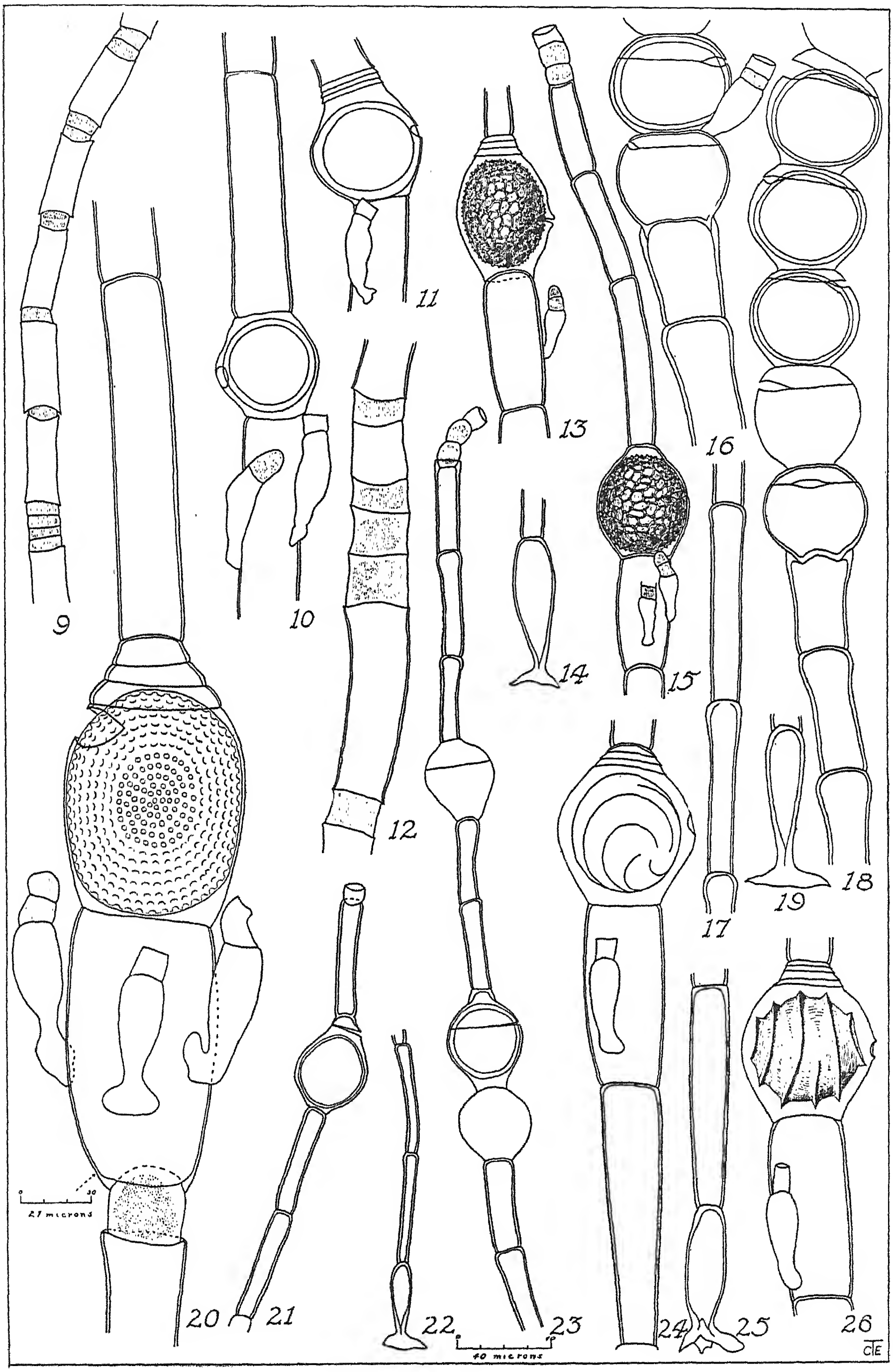

TAFT: OEDOGONIACEAE

INDEX TO AMERICAN BOTANICAL LITERATURE
1931–1935

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Fertilization in the incompatible cross Datura Stramonium × D. Metel

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(WITH PLATES 17 AND 18)

Crossability between species of *Datura* has been a subject of study for some years (Blakeslee, 1933). All the herbaceous species of *Datura* in our collection except *D. ceratocaula* and *D. Metel*, have given viable seeds in some combination with at least one other species. There is, however, considerable variation in the number of successful crosses among them. Successful reciprocal crosses are rare.

Although a cross between two species may not produce viable seeds, the foreign pollen nevertheless may serve as a stimulus for initiating growth of the capsule. Such capsules at maturity may contain only minute dried ovules or small aborted seeds which actually consist of seed coats only.

Inability to obtain viable seeds from some combinations is attributable to various causes. These may be classified into three groups: (1) inability of the pollen tubes to function normally in a foreign style; (2) failure of fertilization; (3) inability of the zygote or of the endosperm to develop, or arrest of their development before maturity.

A detailed discussion of our findings will be arranged according to the main stages in which abnormalities may be a cause preventing formation of viable hybrid seed. As a control, study was made of pollen grains and pollen tubes of *D. Metel* in *intra se* crosses and of *D. Stramonium* in *intra se* crosses. Furthermore, the whole process of fertilization and embryo development in *intra se* crosses of *D. Stramonium* was investigated.

I. POLLEN GRAINS AND POLLEN TUBES

Technique. Methods used to study pollen grains, their germination and the pollen tube growth were as follows: (a) Smear preparations of pollen grains were fixed in Navashin's or in a modified Carnoy's fixative (Satina and Blakeslee, 1935) and stained by the Feulgen method. Details of this latter method are given by Margolina (1932). After treatment in normal or 0.5 normal solution of hydrochloric acid, pollen grains required staining in fuchsin sulphurous acid only ten to fifteen minutes instead of the one to three hours recommended by Margolina for other plant material. (b) For germination of pollen grains and early stages of pollen tube growth

[THE BULLETIN FOR MAY (62: 243–300) WAS ISSUED MAY 1, 1935]

Trankowsky's (1931) method was found to be of great value. Pollen grains were sown on slides covered with a very thin layer of 1% agar with 2% to 12% saccharose. The slides were inverted on glass rods in large Petri dishes to which drops of water were added around the edge of the dishes. Moisture in Petri dishes is the most important factor for germination. To avoid bursting of the growing pollen tubes it was found necessary to keep the slides inverted. This prevents contact of young pollen tubes with water which would condense on the agar. The addition of a certain amount of sugar to Navashin's fixative (a slightly higher percentage of sugar than the one on which the pollen grains grew) prevents the bursting of pollen tubes when they are fixed. After being kept three to five minutes in such a mixture, the slides were placed in Navashin's solution alone. (c) For studying the pollen tube growth in the style, a number of flowers were castrated 24 hours before pollination and kept after pollination at 19.6 to 20°C. All these pollinations were made by Mr. L. F. Williams. At fixed intervals styles were dipped for one to two minutes into water at 60 to 62°C, then placed on a slide and dissected in aceto carmine with glass needles.

The microspore of *D. Metel* seems to develop in the same way as the microspore of *D. Stramonium*. The division of the nucleus in a young pollen grain (fig. 1) to form the tube and generative nuclei occurs before the pollen grain is fully mature. The size and affinity for stain of these nuclei differ considerably (fig. 2). The generative nucleus is smaller and easily found, due to its bright purple color when stained by the Feulgen method. It is cut off from the rest of the microspore by a membrane and forms a distinct cell at one side of the pollen grain. The larger round tube nucleus does not stain so intensely.

The germination of pollen grains can be studied either on the stigma or on the slides by the method just described. For cytological study the latter was preferred. The pollen grain of *D. Metel* begins to swell fifteen to twenty minutes after being sown on the agar slide and kept at 22 to 24°C. Thirty to forty minutes later, pollen tubes begin to grow through one of the pores of the pollen grain membrane. The tube nucleus which is ready to leave the pollen grain changes its shape. It is now oblong, vermiform, sometimes twisted and one of its ends is directed toward the pore (fig. 3). It escapes from the pollen grain before the generative nucleus which has remained almost unchanged in appearance up to this time. Two to four hours later both nuclei were found near each other in the pollen tube. The shape of both is very variable but they are more or less oblong. Further development of the pollen tube was studied in the styles. The generative nucleus of *D. Metel* when crossed *intra se*, as well as that of *D. Stramonium*, divides seven to nine hours after pollination to form the two

male gametes. Figure 4 shows the prophase stage of division of the generative nucleus in *D. Metel.* The division of the generative nucleus at the metaphase stage in the pollen tube of a selfed *D. Stramonium* is shown in figure 5. Twelve chromosomes are seen. The style was dissected and fixed nine hours after pollination. Ten to seventeen hours after pollination the tube nucleus still is closer to the tip of the pollen tube than the two male gametes. Sometimes the distance between the latter and the tube nucleus is very large, in other cases they are close together (fig. 6). The same is true of their distance from the tip of the pollen tube. The shape of the nuclei is also very variable: round or pear shaped, amoeboid or oblong. The position of nuclei in pollen tubes changes when the latter reach the micropyle (fig. 7). The tube nucleus then is found behind the male gametes, the latter are nearer to the tip of the pollen tube. Figure 7 shows part of a section made from an ovule of a control in *D. Stramonium* fixed 29 hours after pollination. The egg apparatus is ready for fertilization:—two synergids near the micropylar end of the embryo sac, the egg cell with the egg nucleus and a very large central nucleus formed from two fused polar nuclei.

The same behavior of nuclei in pollen tubes soon after pollination as well as in more advanced stages of development was found in crosses between *D. Stramonium*×*D. Metel*, except that the division of the generative nucleus took place 3 to 4 hours later. In the styles examined 23 hours after pollination, the length of the pollen tubes reached 5 to 6 cm. They were rather close to the ovule but still in the style. The pollen tube has two male gametes and one tube nucleus. The latter is still closer to the end of the pollen tube (fig. 8). As can be seen from the comparison of pollen tube growth in crosses and controls, no differences could be found except the rate of growth. The pollen tube in crosses grows more slowly than in controls.

II. AND III. FERTILIZATION; THE PROEMBRYO AND ENDOSPERM DEVELOPMENT

A number of capsules of *D. Stramonium* used for control and 111 capsules of *D. Stramonium* pollinated with *D. Metel* were fixed in modified Carnoy (Satina and Blakeslee, 1935) or Navashin's solution. The pollinations were made in four different seasons (January, March, July, September), the first two having been made on greenhouse plants, the second two on field plants. Nearly a half of the 111 capsules were left on the plants to see whether seeds would be developed. Only a few capsules failed to set and dropped within seven to ten days after pollination. Cytological study

was made on 30 capsules which had been fixed at intervals from 22 hours to 8 days after pollination. Sections were cut from 5μ to 10μ in thickness. Seeds were removed from capsules and fixed from 8 to 25 days after pollination. These seeds were also imbedded in paraffin and sectioned. Free-hand sections were made of seeds which had been taken from capsules and fixed 25 to 40 days after pollination. All this material was stained with iron haematoxylin or by means of the Feulgen reaction. The latter was found to be of exceptional value for studying the fertilization process since it is specific for chromatin and leaves other substances in the cell unstained.

II. FERTILIZATION

Guignard studied double fertilization in *D. laevis* in 1902. A detailed study of this process will be given in the present paper. Fertilization in both the cross and control flowers will be described together in order to avoid too much repetition. This process of fertilization seemed to be the same in both cases except for the time required for the pollen tube to reach the embryo sac. Whereas in the cross *D. Stramonium*×*D. Stramonium* the first few pollen tubes entered the micropylar end of the embryo sac 22 to 24 hours after pollination; in the cross *D. Stramonium*×*D. Metel* the first few pollen tubes apparently did not reach the same point until about 44 hours after pollination. In the latter cross no pollen tubes were found in the six ovaries which were fixed successively 19 to 27 hours after pollination. Of three ovules fixed 44 to 47 hours after pollination only one did not have pollen tubes. While it is not known definitely why pollen tubes were not found in these seven capsules it seems probable that they were fixed before the pollen tubes had reached the ovules. In all the other material examined 48 hours and more after pollination, there was only one ovary in which there was no evidence of pollen tube growth having taken place. This older material includes ovules and seeds from 31 capsules.

When a pollen tube reaches an embryo sac it passes through one of the synergids and ruptures in the embryo sac near the egg cell. The two male gametes together with a large amount of the cytoplasm from the pollen tube are released and the latter partly envelops the egg cell. Due to its strong affinity for iron haematoxylin, this mass could be observed during the whole process of fertilization and even later on near the young pro-embryo (figs. 16, 18, 19, 22, 24, 25). One of the male gametes approaches the egg nucleus, while the other approaches the central nucleus lying always close by (figs. 9, 10). Fusion of the egg nucleus with a male gamete rarely occurs at the same time as the fusion of the central nucleus with the other male gamete. It may precede or it may succeed the latter. Figure 11

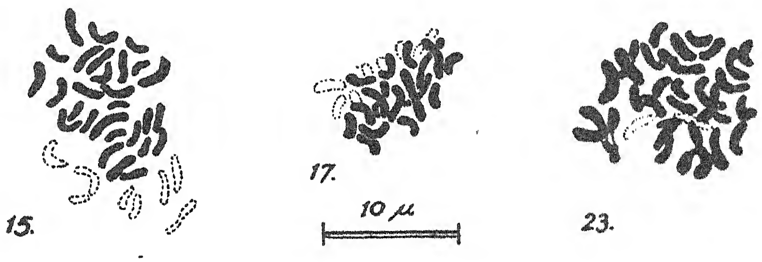
shows an almost completed fusion of the male gamete with the egg nucleus, while the other male gamete had not yet come into contact with the central nucleus. This is true for both cross and control flowers. The shape of the male nucleus is slightly variable, but it seems that when it approaches the female nuclei it is usually round or pear-shaped (fig. 9 to 11). The clearest and best pictures of fertilization were obtained with the Feulgen reaction with which the cytoplasm from the pollen tube, and all other substances, except nuclei present in the embryo sac, remain colorless. (With such dyes as haematoxylin or crystal violet, however, they are strongly stained.) The double fertilization process could be watched step by step from the moment when the male gametes are released from the pollen tube to the moment when they have fused completely with the female nuclei. There is an obvious difference in the chromatic matter of the male and the female nuclei. The sperm nuclei are smaller, have larger chromatic particles and stain more deeply (figs. 9, 10, 11). Their dark purple color contrasts with the faintly stained egg and central nucleus, each of which contains a large stainless nucleolus (figs. 9–13). After a male nucleus has come in contact with a female nucleus, it elongates on the surface of the latter, then gradually is incorporated within it (figs. 11–13). It remains visible for a considerable length of time although its outline and area become increasingly vague. A very small and faintly stained nucleolus begins to form in the remains of the male nucleus (fig. 11). Toward the end of the fusion there remains a thin, oblong, more darkly stained area at the periphery of the egg and central nuclei (fig. 13). Fusion is considered complete when these nuclei stain uniformly throughout. Thereafter these nuclei may be called the zygote or fertilized egg and the endosperm nucleus respectively. The former is a diploid nucleus, the latter a triploid.

There seemed to be no visible difference between fertilization in cross and in control flowers of *D. Stramonium* even though this process was closely observed in the hope of detecting differences between them. Fertilization in the cross between *D. Stramonium* and *D. Metel* takes place and the fact that fusion occurs cannot be doubted.

It should be added that the second synergid in the embryo sac remains visible until the end of the fertilization process (fig. 11) and then disintegrates. The pollen tube after releasing the male gametes, always contains two so-called x-bodies (fig. 11). They are deeply stained by the Feulgen reaction and must therefore contain chromatin. They are evidently disintegrating nuclei; one belongs to the synergid through which the pollen tube grew, and the other is the tube nucleus of the pollen tube.

III. THE PROEMBRYO AND ENDOSPERM DEVELOPMENT

After fertilization is complete in the cross *D. Stramonium* × *D. Metel* the zygote and endosperm nuclei divide, but the amount of time that elapses between fertilization and cell division is variable. Several hours always pass by before the latter occurs. It is the triploid endosperm nucleus which starts to divide. Various stages of its division were found in capsules taken from cross pollinated flowers 68–72 hours after pollination. In other ovules division of the endosperm nucleus did not begin until four days after pollination. In exceptional cases the division started on the fifth day.



Figures at a magnification of 1800 diameters.

Fig. 15—*D. Str.* × *D. Metel:* 36 chromosomes in metaphase plate of an endosperm cell, 5 days after pollination.

Fig. 17—*Same:* 24 chromosomes in metaphase plate of a zygotic nucleus.

Fig. 23—*D. Str.* × *D. Str.:* 36 chromosomes in metaphase plate of an endosperm cell, 7 days after pollination.

Figure 14 is a drawing of a section through one of the ovules fixed three days after pollination. It shows a pollen tube which has grown through the micropyle, an undivided zygote and two endosperm cells. The presence of these two separate endosperm cells is in agreement with Guignard's (1902) observations that the endosperm in *D. laevis* (our white inermis stramonium) has no stage of free nuclear division. The second division takes place soon afterwards but does not always occur simultaneously in the two daughter nuclei. Other divisions follow and soon a number of normal appearing cells are formed.

Each cell contains a rich amount of cytoplasm and a large nucleus. Especial attention was devoted to the division process in these endosperm cells; it seemed to be normal. Thirty-six chromosomes were counted in numerous endosperm cells at metaphase stage. It is thus seen that the endosperm cells were 3n, each of them having one paternal and two maternal chromosome sets (fig. 15).

Normal appearing endosperm cells without any visible trace of dis-

integration are to be found in young capsules fixed from three to six days after pollination. They predominate also at the seventh day after pollination and in some seeds at the eleventh or thirteenth day. However, disintegration sometimes occurs earlier—at the sixth day after pollination. Figure 20 shows such a case; the disintegration only begins in the proembryo but the endosperm cells are already dead. The epithelial cells which surround the embryo sac are of enormous size in comparison with those of normal seeds or even with those of hybrid seeds in which the disintegration of the endosperm has been delayed (fig. 21). In the majority of seeds fixed on the eighth, ninth to fourteenth day after pollination all endosperm cells are usually dead and their resorption proceeds rapidly.

Division of the zygotic nucleus begins usually on the fifth, sometimes on the fourth day after pollination, that is, one or two days after the endosperm nucleus has completed four to five divisions. Figure 16 shows such a case. It is a section from an ovule in which 18 endosperm cells are already formed and the zygotic nucleus goes through its first division. It contains 24 chromosomes in metaphase (fig. 17). Figure 18 shows a young proembryo with two cells, figure 19 shows one with four cells. They were found among a large number of other proembryos in a capsule fixed five days after pollination. In capsules six to seven days old, proembryos with two to four cells are common while those with five and six cells are rare. A proembryo with as many as eight cells was found only once. It is evident that, though fertilization can take place and two or at most three successive divisions in the young sporophyte can occur, something prevents further growth.

Disintegration proceeds independently in the proembryo and in the endosperm cells. Frequently the proembryo has been resorbed before the endosperm begins to disintegrate and a cavity approximately equal to its size and shape results (fig. 21). In other cases the proembryo is still present while the endosperm is partly resorbed (fig. 20).

The early stages of development of the endosperm in *D. laevis* have been given by Guignard (1902), and a detailed study of the proembryo development in *D. Stramonium*, *D. laevis* and *D. Tatula* (which may be included in *D. Stramonium*) was made by Souèges (1922). No detailed description of proembryo nor of endosperm development in controls need be given in the present paper, since the results confirm the findings of these authors. Only few details, such as chromosome counts in the endosperm cells, may be added. Figure 22 shows the division of an endosperm nucleus and an undivided zygote, figure 23 has a metaphase plate from a triploid endosperm cell in which 36 chromosomes can be counted. The first drawing was made from a capsule four days old, the second from a capsule seven

days old. A three-celled proembryo in which the lower cell is dividing is shown in figure 24, and a four-celled proembryo is shown in figure 25. Both proembryos were found in a capsule five days old. If we compare the development of the endosperm and proembryo in the cross *D. Stramonium* ×*D. Metel* with *intra se* crosses of *D. Stramonium* it will be seen that no visible differences are detectable at early stages. The division of the zygotic nucleus occurs in both at the same relative time. The endosperm nucleus divides first, then after about four or five divisions have taken place the zygotic nucleus starts dividing. The zygotic nucleus contains 24, the endosperm nucleus 36 chromosomes.

Although the early stages of growth appear to be indistinguishable, a difference is noticeable in the rate of further development. Crosses of *D. Stramonium* with *D. Metel* develop slower than those of the control. It is clearly seen six to seven days after pollination. At this time the proembryo of the control consists of 16 to 30 cells while the proembryo of the cross has only four to six cells. The same difference in rate of development was observed in the two kinds of endosperm. That of the control showed about 70–120 cells in transverse section while comparable figures for the cross are 18–30 cells. This latter number corresponds to a total of 80 to 90 cells for the endosperm of the cross. This difference in number of cells increases rapidly in later stages because of the continued division of the proembryo and endosperm in the control, while in the cross there is a gradual arrest of development. In later stages only isolated dividing cells may be found in the disintegrating endosperm of the cross. The division of the proembryo stops earlier. By the end of the second week, except in the few cases mentioned above, large cavities, due to resorption, are found in place of the seed proper. It is of interest that the seed coat develops normally and does not seem to be affected by the disintegration of the seed.

Michaelis (1925) reported the embryological history in crosses between *Epilobium* species, but did not study their chromosomes. In certain combinations the hybrid proembryo developed normally but the seed failed to germinate. In others a number of irregularities accompanied the development of the proembryo (no cell wall formation in the proembryo after division, giant cells in the endosperm, etc.). In a certain combination the proembryo degenerated at early stages after a few cells had been formed. This latter type resembles the data reported in this paper.

As has been shown, failure to form viable seeds in the cross *D. Stramonium*×*D. Metel* is not due to irregularities of pollen-tube growth in the foreign style nor to lack of fertilization. Both female nuclei fuse with male gametes, forming a 2n zygote and a 3n endosperm. In these cells the occurrence of the first division after fertilization is not surprising since the

chromosomes are already split in anticipation of this division. But the fact that chromosomes of *D. Metel* participate in further divisions indicates that they can grow and divide in the *D. Stramonium* cytoplasm, at least for a limited number of divisions.

The later stages observed in both proembryo and endosperm of these hybrid seeds give the impression that disintegration of the cells prevents further divisions of the chromosomes rather than that failure of chromosomes to divide is a primary factor preventing further development. The present paper is one of a series on the species problem in the genus *Datura*. It gives information regarding the stages in an incompatible cross at which development is arrested but leaves to later investigations the mechanisms by which this block to hybridization is accomplished.

SUMMARY

1. In mature microspores of *D. Metel* and *D. Stramonium* there is a smaller generative nucleus and a larger tube nucleus.

2. In the cross *D. Stramonium*×*D. Metel* two male gametes are formed by division of the generative nucleus in pollen tube.

3. One male gamete fuses with the egg nucleus, the other with the central nucleus, as in the parent species.

4. The zygote is 2n and the endosperm 3n, as in control (*D. Stramonium*).

5. Endosperm begins to divide before the zygote.

6. Cells of the endosperm appear normal up to about the seventh day, when disintegration begins.

7. Proembryos up to about the fifth or seventh day appear normal but do not form more than eight cells after which disintegration and resorption occurs.

8. Disintegration may occur first in either the proembryo or endosperm.

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Explanation of figures 1–13

Figures, except when noted, at a magnification of 900 diameters.

c—central nucleus; g—generative nucleus; p—pollen tube; s—synergid; t—tube nucleus; x—X-body; ♂—male gamete; ♀—egg nucleus

Fig. 1—*D. Stramonium:* 12 chromosomes, metaphase in microspore.

Fig. 2—*D. Metel:* generative and tube nuclei in microspore.

Fig. 3—*Same:* germination of microspore: generative and tube nuclei. Microspore fixed 1½ hour after having been placed on agar.

Fig. 4—*Same:* generative nucleus at prophase stage in pollen tube, 7 hours after pollination. ×1050.

Fig. 5—*D. Str.:* generative nucleus at metaphase stage in pollen tube showing 12 chromosomes, 9 hours after pollination.

Fig. 6—*Same:* 2 male gametes and tube nucleus in pollen tube, 9 hours after pollination.

Fig. 7—*D. Str.×D. Str.:* part of an embryo sac before fertilization, pollen tube in micropyle, 2 male gametes near the tip of the pollen tube; tube nucleus behind; 2 synergids, egg cell and central nucleus; 29 hours after pollination.

Fig. 8—*D. Str.×D. Metel:* two male gametes and tube nucleus in pollen tube, 23 hours after pollination.

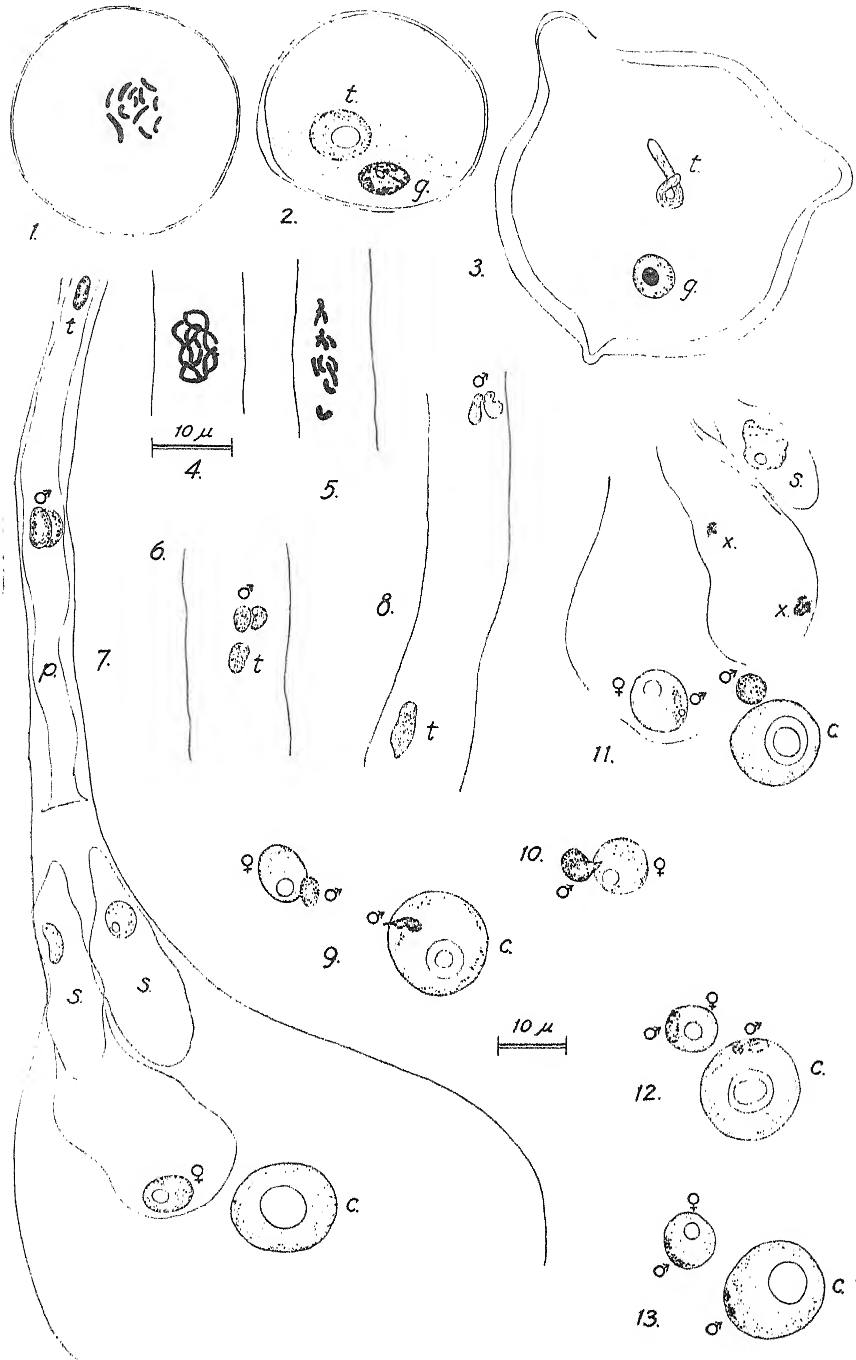
Fig. 9—*Same:* double fertilization, male gametes in contact with egg and central nuclei, 68 hours after pollination.

Fig. 10—*D. Str.×D. Str.:* male gamete in contact with egg nucleus, 29 hours after pollination.

Fig. 11—*Same:* double fertilization, fusion almost completed in egg nucleus; male gamete approaches the central nucleus; two *X* bodies in pollen tube, 1 synergid; 29 hours after pollination.

Fig. 12—*D. Str.×D. Metel:* double fertilization; fusion almost completed, 68 hours after pollination.

Fig. 13—*D. Str.×D. Str.:* double fertilization, fusion almost completed, 29 hours after pollination.



SATINA AND BLAKESLEE: FERTILIZATION IN DATURA

Explanation of figures 14, 16, 18–22, 24 and 25

Figures, except when noted, at a magnification of 900 diameters.

e—endosperm; p—pollen tube; z—zygote

Fig. 14—*D. Str.* × *D. Metel:* 2 endosperm cells, undivided zygote, pollen tube, 3 days after pollination. ×200.

Fig. 16—*Same:* division of zygotic nucleus, two endosperm cells; lower cell at anaphase, 5 days after pollination.

Fig. 18—*Same:* 2 celled proembryo, 5 days after pollination.

Fig. 19—*Same:* 4 celled proembryo, 5 days after pollination.

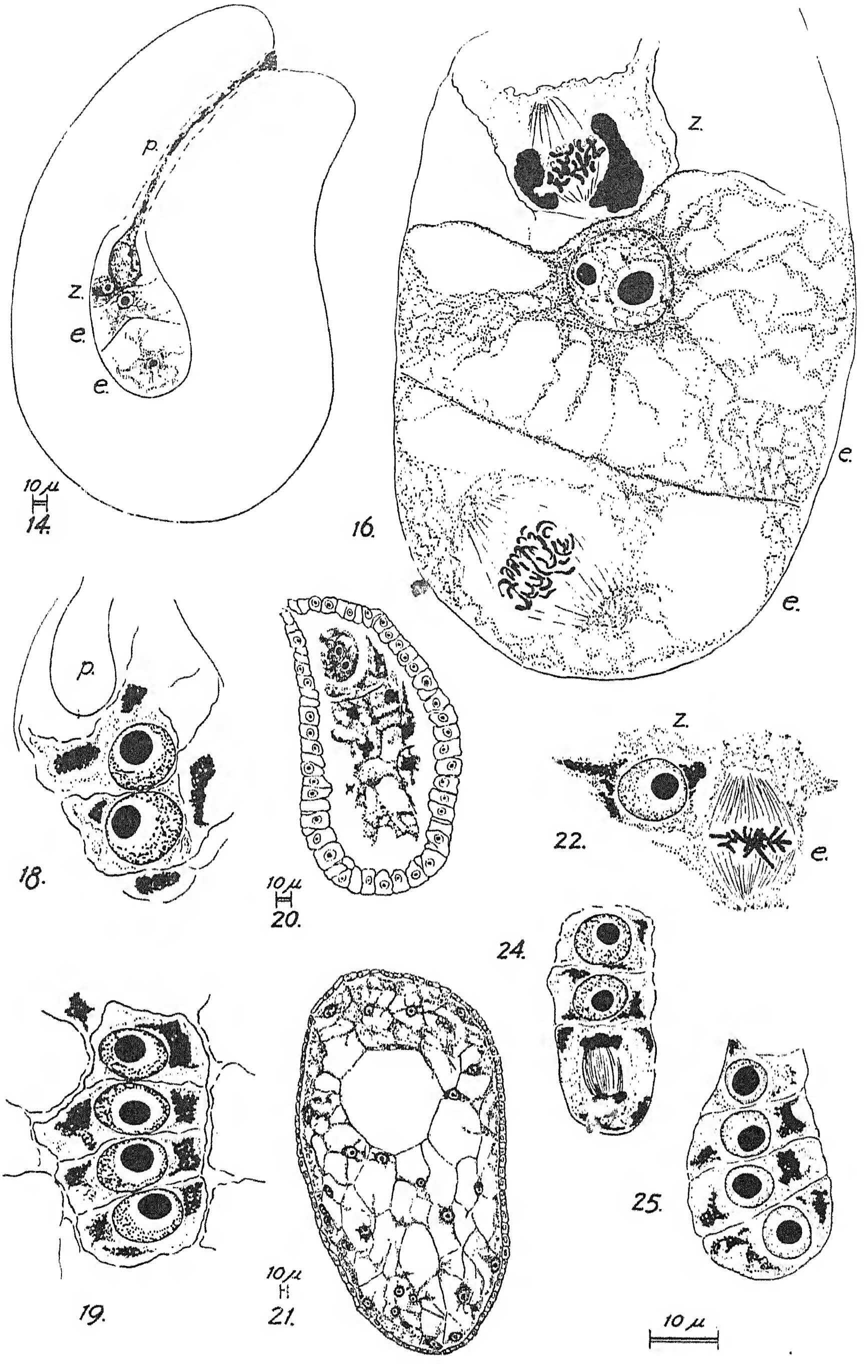
Fig. 20—*Same:* advanced stage of disintegration in endosperm and early stage of disintegration in proembryo; enlarged cells of the epithelium around the embryo sac, 6 days after pollination. ×200.

Fig. 21—*Same:* normal endosperm with proembryo entirely resorbed; 11 days after pollination. ×100.

Fig. 22—*D. Str.* × *D. Str.:* 1st endosperm division showing only part of the chromosomes; zygote undivided, 4 days after pollination.

Fig. 24—*Same:* 3 celled proembryo, 5 days after pollination.

Fig. 25—*Same:* 4 celled proembryo, 5 days after pollination.



SATINA AND BLAKESLEE: FERTILIZATION IN DATURA

Differential distribution of a phytohormone in the developing leaf of Nicotiana, and its relation to polarized growth

George S. Avery, Jr.

(WITH FIVE TEXT FIGURES)

INTRODUCTION

A rapidly increasing interest in plant growth hormones (variously referred to as Wuchsstoff, growth substance, growth regulator and auxin) has been aroused since Went (1928) showed that quantitative determination was possible by the use of *Avena* coleoptiles. Supplementary (Thimann 1934, Went, 1934) or other methods suggested more recently have extended the range of possibilities.

The phytohormones so far reported seem closely linked with growth by cell enlargement, although Almoslechner (1934) reports distinctly different hormones for cell enlargement (Wuchsstoff A) and cell division (Wuchsstoff B) in yeast. Kögl has recently (1935) given evidence that minute amounts of a hormone which he designates as "Biotin *a*" may accelerate cell division in yeast as much as 1400%, a figure many times greater than that given by Almoslechner for Wuchsstoff B.

The generic term *auxin* for phytohormones which bring about cell enlargement has been proposed by Kögl. The advantage of this uniform terminology is clear from the following. Auxin *a* and *b* have been isolated from a number of plant materials (Kögl, Erxleben and Haagen-Smit, 1934*a*) and crystallized in pure form. Auxin *a* has the chemical formula $C_{18}H_{32}O_5$, and auxin $b = C_{18}H_{30}O_4$. Their structural formulae have been reported recently (Kögl and Erxleben, 1934). A substance identical with β-indolyl-acetic acid ($C_{10}H_9O_2N$) has been isolated from urine and from yeast and the name *heteroauxin* has been suggested for it (Kögl et al, 1934*b*, 1934*c*).

Most investigations on growth effects of auxin have been concerned with *Avena* seedlings, although a wide variety of materials have been subjected to examination in the past two years. The presence of auxin in leaves has been demonstrated in numerous instances for *Avena* (the coleoptile is interpreted as the second, or sheathing leaf of the plant, Avery, 1930), *Vicia faba* (Thimann and Skoog, 1934), and *Ipomoea* (Koning, 1933) But there has been no work on its distribution in relation to growth of foliage leaves. The purpose of this study was, first, to determine the concentration of auxin in leaves of varying ages: second, to determine whether differential distribution of auxin within the leaf might be correlated with differential growth intensity, or whether all parts of the leaf have it in

equal concentrations; third, to find whether it accumulates in certain portions of the leaf, or is transported in certain tissues, i.e., vascular tissue, etc. (next to nothing is known of its path of transport in mature plants); fourth, to determine whether its movement is polar, as has been demon-

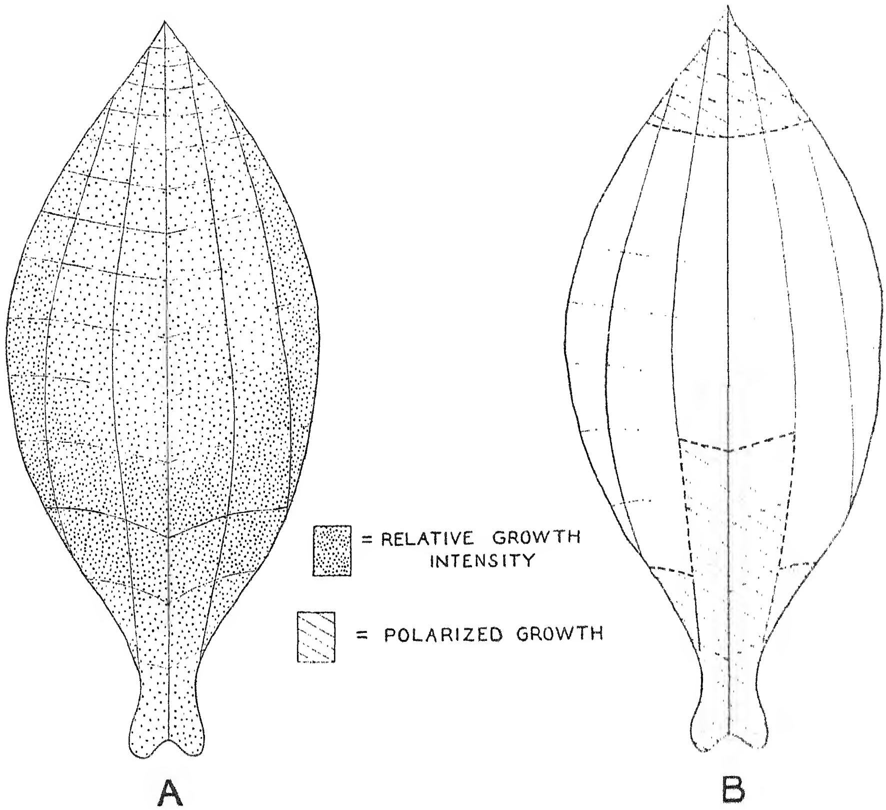


Fig. 1. After Avery, 1933. A, the density of the dots indicates relative growth intensity (*localized growth*) in the different portions of a developing leaf. The marginal and basal regions undergo the greatest growth. B, the segments indicated in the distal and proximal portions of the leaf show a relatively greater increase in length than in width. While this *polarized growth* is not so pronounced at the apex, it is very striking at the basal end of the leaf (where it is correlated with higher concentrations of auxin).

strated in *Avena* coleoptiles; fifth whether it is actually a limiting factor in leaf growth, and sixth, if a limiting factor, whether it is influencing cell division, cell enlargement, or both.

Leaves of *Nicotiana* were chosen for study because of their large size, and because their growth has already been investigated. It has been shown

(Avery, 1933) that relative growth rates differ in different portions of the leaf, and that growth intensity (*localized growth*) is greatest near the proximal end and at the margins (fig. 1 A). It has been shown also that the distal and proximal portions of the leaf, more particularly the latter, show a relatively greater increase in length than in width (fig. 1 B, *polarized growth*). Is auxin in part responsible for either localized or polarized growth?

MATERIALS AND METHODS

Two species and several varieties of *Nicotiana* were used in these experiments: *N. sylvestris* Speg. & Comes, pedigree number 34100; F_1 plants of *N. Tabacum*×tetraploid *N. sylvestris* no. 34334; *N. Tabacum* L., varieties *purpurea* (no. 34042), Connecticut Broadleaf (no. 34043) and R. E. Clausen's Broadleaf (no. 34045). Most were supplied through the kindness of Drs. Thomas H. Goodspeed and Helen Mar Wheeler of the University of California.

Young plants were removed from the field near Berkeley on July 2, and were replanted in 8 inch pots in the greenhouse in Pasadena on July 5, 1934. There were from five to eight good sized leaves on each plant at the time of transplanting, and three to four weeks later most of the plants had from ten to eighteen leaves.

The main procedure followed for the extraction of auxin was the diffusion method of F. W. Went (1928). Definite portions were cut from the leaf and rolled into compact cylinders which were tied with fine copper wire (fig. 2 A, B, C). The proximal cut end was touched with 10% gelatin and the cylinder then placed on the standard agar block (Dolk, 1930). Diffusion was allowed to continue for the usual two hour period in a moist chamber. Where the diffusion method was used on whole leaves of a length greater than six or eight centimeters, the leaves were hung from a rack in a large moist chamber, and the agar block was attached to the cut petiolar end of the suspended leaf.

The chloroform method of Thimann (1934) was used as a check on the diffusion method, and in other instances where it seemed desirable to extract all the auxin present at any given time. It consists, in brief, of immersing the fresh material in chloroform, adding a small amount of hydrochloric acid, and grinding thoroughly. The chloroform layer containing the auxin is separated from the residue, and is then evaporated off. The lipoidal material remaining is taken up in a very small volume of water to which is added an equal volume of 3% agar. The standard size block is then cast from this.

Quantitative determinations of the extracted auxin (from both the

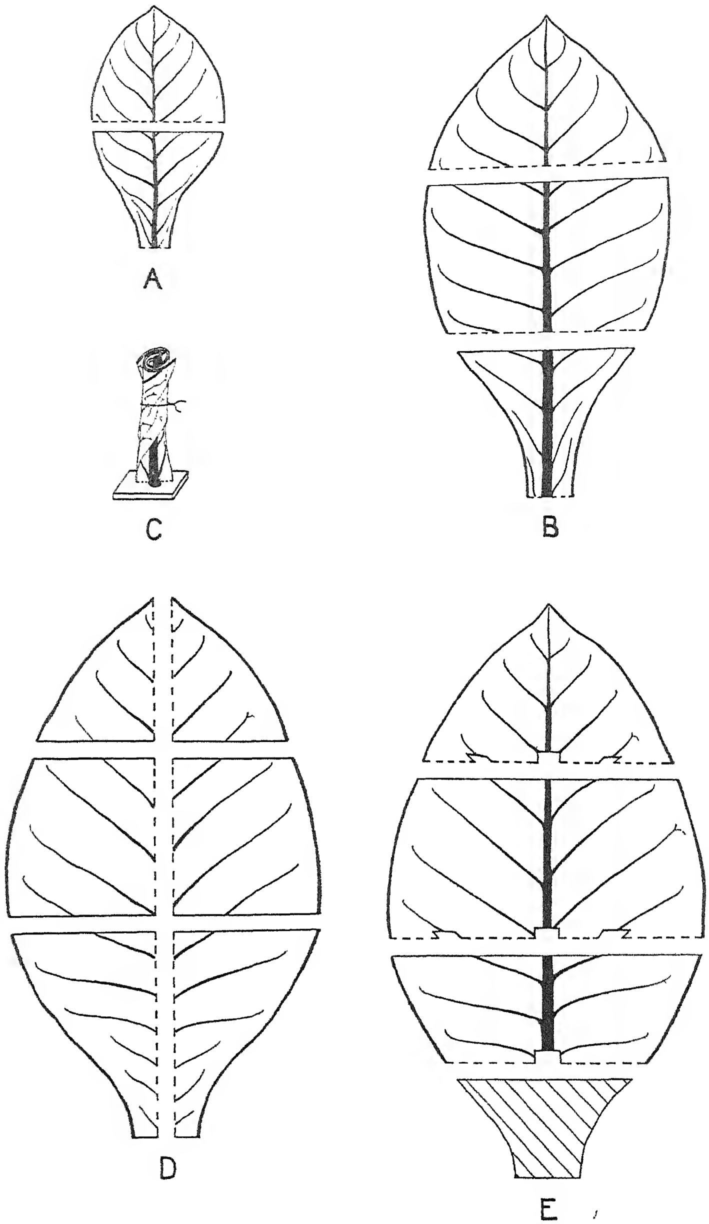


Fig. 2. Diagrams showing how young (A) and older (B) leaves were cut into segments, and how the auxin was "diffused" into the agar block (C); D shows how the midrib was removed so that it and the remainder of the leaf might be tested separately; E shows how the midrib and large lateral veins were cut back in one experiment, so as not to come in contact with the agar. The portion of the leaf placed in contact with the agar block is indicated by a discontinuous line (- - -).

diffusion and chloroform methods) were made according to the Went (1928) technique. The test depends upon the curvature produced in decapitated *Avena* coleoptiles when small segments of the above mentioned agar blocks containing auxin are applied to one side of the long stump remaining after decapitation. It has been shown (Thimann and Bonner, 1932, and van der Wey, 1932) that the result depends on relative *concentration* rather than upon the *amount* of the auxin present in the blocks. All tests were carried out in a dark room especially designed to maintain temperature at 25° to 27° C., and relative humidity at approximately 90%.

Results are given in "plant units" (Dolk and Thimann, 1932) where 1 *p. u.* equals 1° curvature of the coleoptile stump, brought about in 110 minutes by the presence of the auxin contained in the agar block. Such a plant unit is equal to only four-tenths of the *Avena* unit ("AE") of Kögl, Haagen-Smit and Erxleben (1933).

In certain experiments heteroauxin, synthesized by Dr. K. V. Thimann, was thoroughly mixed with lanolin (90 mg. to 10 gms.) and applied externally to leaves, similar to the lanolin method of Laibach (1933) in which orchid pollen was used as a source of the auxin.

CONCENTRATION OF THE AUXIN IN YOUNG AND OLDER LEAVES

The terminal inflorescences were just appearing at the tips of the plants as the leaves of each variety were tested. The leaves immediately below were still very young, while those from successively lower levels were correspondingly older (table 1). Each figure represents the average of two leaves, and the number of plant units are given both for the leaf as a whole, and on a per square centimeter basis.

It is clear that the very young leaves, notably the first two below the embryonic inflorescence, are high in growth substance. There were only nine leaves on the plants tested July 13, and the upper five of these were still undergoing appreciable growth. The lower four were increasing in length only slightly, and were therefore interpreted as being nearly mature. This greater degree of maturity is correlated with a rapid dropping off in the concentration of the auxin. Corresponding results were obtained from tests on leaves of another variety nearly two weeks later. In this case there were more leaves on the plants, and the lower leaves were mature. Complete maturity is correlated with a total absence of auxin.

It seems reasonable to conclude from these tests that auxin is present only in growing leaves and that its concentration is roughly inversely proportional to the age of the leaf.

TABLE 1

Auxin concentration in the inflorescence, and in leaves of various ages from different levels on the stalk. Concentrations are given in plant units ("p.u.")[1]

LEAF NO. BELOW INFLORESCENCE	N. TABACUM VAR. PURPUREA, JULY 13			N. TABACUM VAR. CONNECTICUT BROADLEAF, JULY 25		
	AVERAGE AREA PER LEAF IN SQ. CM.	TOTAL P.U.	AVERAGE P.U. PER SQUARE CM. OF LEAF	AVERAGE AREA PER LEAF IN SQ. CM.	TOTAL P.U.	AVERAGE P.U. PER SQUARE CM. OF LEAF
Infloressence		32			53.4	
1	5.00	46.5	9.37	1.32	45.9	34.8
2	6.61	55	8.32	5.09	56.5	11.10
3	17.8	58.5	3.28	20.19	60	2.97
4	38.12	40	1.04	27.54	54	1.95
5	31.2	37.5	1.20	55.35	39.5	0.713
6	44.4	24	0.54	109.77	38.5	0.350
7	61.0	26	0.425	120.93	29.5	0.243
8	86.93	9.9	0.115		11	
9	140.67	18	0.127	247.83	11.4	0.045
10				301.03	11.5	0.038
11				277.80	0.0	
12				187.12	0.0	
13				139.61	0.0	
14				158.51	0.0	
15				164.48	0.0	

[1] One plant unit equals 1° curvature of the coleoptile stump, brought about in 110 minutes by the presence of the auxin contained in the agar block.

DIFFERENTIAL DISTRIBUTION OF AUXIN IN THE LAMINA OF YOUNG AND MORE NEARLY MATURE LEAVES

The concentration gradient from tip to base of leaf

Leaves at various stages of development, from very young to nearly mature, were divided into halves, thirds, or quarters and tested by the

diffusion method (fig. 2). Auxin is present in all portions of the leaf in young rapidly growing leaves such as A–C, F and G (table 2 and fig. 3),

TABLE 2

Distribution of auxin in different portions of the leaf in leaves of varying ages.

N. TABACUM VAR. PURPUREA	DATE	AREA IN SQ. CM.	TOTAL P.U.	P.U. PER SQ. CM.
A. Leaf 4.5 cm. long[2]				
terminal half	July 13	3.45	24.9	7.21
basal half		3.67	42	11.44
B. Leaf 8 cm. long[2]				
terminal half	July 13	13.70	27	1.97
basal half		14.61	45.9	3.14
C. Leaf 10 cm. long[2]				
terminal third	July 13	6.58	20.4	3.10
middle third		15.48	36.9	2.38
basal third		9.77	72	7.26
D. Leaf 18 cm. long (practically mature)				
terminal quarter	July 6		0.0	
upper middle quarter			0.0	
lower middle quarter		32.68	20.4	0.63
basal quarter		15.03	33.6	2.23
N. TABACUM×N. SYLVESTRIS				
E. Growing point,[2,3] (with accompanying leaves up to 5 cm. long)	July 22, 23		112.8	
F. Leaf 9 cm. long[3]				
terminal quarter	July 18	5.80	24	4.13
upper middle quarter		11.35	82.2	7.24
lower middle quarter		10.12	96	9.48
basal quarter		4.9	130.2	26.57
G. Leaf 13 cm. long[3]	July 18			
terminal quarter		10.90	21	1.92
upper middle quarter		17.93	72	4.01
lower middle quarter		19.74	78	3.95
basal quarter		9.54	141	14.77

[2] Data from average of 2 leaves.

[3] There was a total absence of auxin in growing points and leaves of plants kept in darkness 5 days before testing. All such duplicate tests were on material of size and parentage comparable to E–G.

but is unequally distributed. There is a distinct gradient from the tip to the base of the leaf, the concentration being much higher near the base. In a nearly mature leaf, such as D, the auxin has disappeared completely from the distal half, while the proximal portion still has a low concentration present.

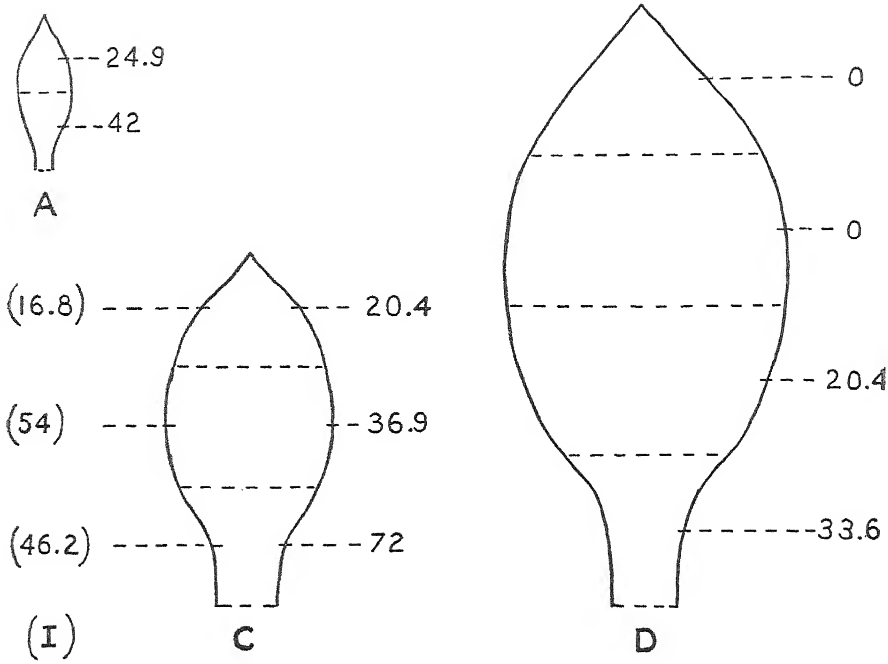


Fig. 3. Diagrams of young (A) and older (C and D) leaves, showing relative concentrations of the auxin in different portions. All figures are in plant units (*p. u.*) and the leaves diagrammed are those similarly lettered in table 2. The data in parentheses are taken from leaf I, table 3; this leaf had been in darkness for ten days, followed by one day in the greenhouse. The auxin concentration gradient shown in A and C is dependent upon accumulation of the auxin in the midrib and its movement toward the base of the leaf (in contrast with leaf I, in which accumulation has not had time to take place). Note its eventual disappearance at the distal end (D) as the leaf grows older.

The chloroform extraction method was used to check the above results. On July 21, three leaves were removed from near the middle of the stalk of a plant of *N. sylvestris*. The leaves averaged 26 centimeters long, and were cut into quarters, rather than into thirds as shown in figure 2, B. The yield in plant units was as follows:

terminal and upper
middle quarter......(average)..... $\begin{cases} 0.17 \textit{ p. u.} \text{ per sq. cm., or} \\ 5.75 \textit{ p. u.} \text{ per gram green wt.} \end{cases}$

lower middle quarter . . . . not tested

basal quarter . . . . {0.8 *p. u.* per sq. cm., or 9.43 *p. u.* per gram green wt.

Thus the concentration of the auxin as shown by the chloroform method corresponds with that of the diffusion method recorded for leaves A–G in table 2.

The fact that there is a definite concentration gradient from tip to base of leaf, and that the auxin tends to disappear distally as the leaf approaches maturity, might be interpreted in two possible ways: either there is a greater amount formed in the proximal portion of the leaf, or, it is formed approximately equally throughout the lamina, but is accumulated in the proximal portion.

Accumulation and transport

Scattered bits of evidence pointing to accumulation and transport in veins were verified by the following tests. On July 26, the midrib and main lateral veins of a large but still growing leaf of the variety Connecticut Broadleaf (28 cm. long) were cut away from the remainder of the lamina and tested separately by the chloroform method:

	WEIGHT	TOTAL YIELD OF AUXIN	AUXIN YIELD PER GRAM GREEN WEIGHT
Midrib and main lateral veins	2.4 grams	144 p.u.	60 p.u.
Intervenous portions of leaf	2.1 grams	57 p.u.	27.14 p.u.

The intervenous portions yielded less than half the auxin shown to be present in the veins.

In another experiment (diffusion method) on July 27, two leaves of *N. sylvestris* were used, each being about 18 cm. in length. The lateral veins were cut from the intervenous portions and midribs, and tested separately: 11 lateral veins taken from the distal half of the leaf showed no appreciable concentration of the auxin; 12 lateral veins taken from the proximal half of the leaf gave 19.8 *p. u.* (both leaves); intervenous material from these same leaves showed no appreciable concentration. The midribs from the same two leaves were divided into three equal lengths and the proximal 3 cm. of each of these lengths was tested: distal 3 cm., negligible; middle 3 cm., 37.2 *p. u.* (both leaves); proximal 3 cm., 43.2 *p. u.* (both leaves).

It will be shown that auxin occurs in approximately equal concentrations in the intervenous regions whether it be at the tip or the base of

growing leaves. This evidence, together with the above data, indicates that accumulation and transport take place largely in the midrib and main lateral veins.

Movement of the hormone is polar

On July 17 two middle sized rapidly growing leaves were cut into thirds, and the *distal* end of each third was applied to the agar block (the reverse of the usual method of placing the proximal end on the block for diffusion). The results were negative! That the movement of the auxin is strictly a polar phenomenon has been reported in several instances by other investigators.

In the leaf shown in figure 2, D, the hormone moved inward from the margin of the leaf toward the midrib. In a similarly prepared leaf, the margin was also cut off and the outer cut edge placed in contact with the agar for diffusion. No yield was obtained. From such results it is clear that the direction of transport is from tip toward base of leaf, and from lateral veins in toward the midrib.

PRODUCTION OF THE AUXIN IN YOUNG GROWING LEAVES

The material for this series of experiments consisted of F_1 plants of *N. Tabacum*×*N. sylvestris*. Foregoing data suggested that the auxin probably was being produced throughout the leaf, even though accumulation and transport were taking place largely in the veins.

The experimental evidence shows (see footnote 3, table 2) that when plants are kept in darkness for a few days before testing, the auxin disappears from the growing point and leaves. The growing point recovers its usual concentration of auxin after a day in the greenhouse, as shown in table 3.

Leaves show a similar recovery but do not have time to accumulate an appreciable amount of the hormone in their proximal portion. In leaves I, J, and K which received this treatment, the central region of the leaf appears to be producing a greater amount of the auxin than corresponding portions of control leaves L and M. If computed on the basis of concentration per square centimeter of lamina, the results are roughly of the same order in both the experiment and the controls. It is clear from this that neither total concentration nor calculations based on area necessarily give a true picture of the results. The explanation for this lies in the differing proportions of midrib and intervenous tissues in different parts of the leaf; for example, the proportion of intervenous material to veins is quite different at the tip, middle, and base of the leaf (fig. 2, B). If computed on the basis of green weight, the direction of the concentration gradient is

TABLE 3

Distribution of the auxin in different portions of leaves. Plants were kept in darkness ten days, then in the greenhouse one day before testing. Leaves L and M were controls. All data for "lamina" include the midrib.

N. TABACUM×SYLVESTRIS F1 JULY 25 (PLANTS PLACED IN DARKROOM FOR 10 DAYS, THEN 1 DAY IN GREENHOUSE)	AREA OF LAMINA IN SQ. CM.	WEIGHT IN GRAMS	TOTAL P.U.	P.U. PER SQ. CM. OF LAMINA	P.U. PER GRAM GREEN WEIGHT
Growing point, with accompanying leaves up to 4.5 cm. long			109.8		
I. Leaf 10 cm. long growing rapidly:					
terminal third of leaf	8.5	0.15	16.8	1.97	112
middle third	14.9	0.55	54	3.62	98.2
basal third	7.6	0.45	46.2	6.07	102.7
J. Leaf 17.5 cm. long still growing, but not rapidly:					
terminal quarter of leaf	14.19	0.26	22.2	1.56	85.4
upper middle quarter	31.93	1.5	66	2.06	73.5
lower middle quarter	20.51	1.5	54	2.63	73.5
lower quarter	7.87	0.74	34.2	4.34	46.2
K. Leaf 18 cm. long, still growing:					
terminal third	29.7	0.55	22.8	0.76	41.4
middle third	44.2	1.3	51.6	1.16	39.7
basal third	12.7	1.2	32.4	2.55	27
(plants grown in greenhouse, same hybrid, July 25)					
L. Leaf 16 cm. long, still growing:					
terminal third	27.5	0.5	0.0	0.0	0.0
middle third	38.3	1.25	43.8	1.4	35
basal third	15.6	1.1	70.8	4.5	64
M. Two leaves, one 16, the other 18 cm. in length:					
segment from terminal portion—*average per leaf*	14.4	.425	27.5	1.9	64.7
strip across middle portion of leaf	21.15	.435	47.5	1.97	100.0
strip across leaf about 3 cm. above base	12	.375	52.8	4.4	139.1

reversed in leaves I, J, and K of leaves which were taken from dark treated plants (table 3). With the midrib adding considerable weight to the basal portion of the leaf and the leaf having had little opportunity to accumulate the auxin, it might well be expected that the concentration per gram of green weight would be proportionally lower in this region. Control leaves L and M, on the other hand, show the same sort of gradient as leaves A–G (table 2).

In order to further test whether the auxin is produced in approximately equal concentrations throughout the lamina, a leaf 12 cm. in length (*N. Tabacum*×*N. sylvestris*) was divided into thirds on July 24. Its midrib and large lateral veins were cut back so they would not be in contact with the agar at the time of diffusion (fig. 2, E). Any diffusion of the auxin which might take place should therefore come from the so-called intervenous regions, where only small veins are present. Diffusion was allowed to go on for four hours, or double the usual length of time. The yield for the distal third was 27 *p. u.*, the middle third 31 *p. u.*, and the proximal third 31 *p. u.* Another leaf of the same parentage, 13 cm. in length, was cut into thirds on July 24. The midrib was entirely removed (fig. 2, D) and the cut edge nearest the midrib was placed downward on the agar. The main lateral veins were left intact. After four hours diffusion the segments from the middle of the leaf gave 40 *p. u.*, those from the proximal end, 41. The terminal segments did not give satisfactory tests.

The results from this series of preliminary experiments show that the hormone is *produced* in approximately equal amounts over the whole lamina, a fact that is usually masked by the *accumulation* which takes place at the proximal end of the midrib when plants are growing under ordinary periods of daylight and darkness.

IS THE PRESENCE OF THE AUXIN A LIMITING FACTOR IN LEAF GROWTH?

Growing leaves of plants which were kept in darkness for ten days showed evidence of tension between the midrib and the lamina. The proximal half of the midrib continued to elongate, and arched upward, while the lamina exerted a restraining influence. The result was a pronounced bulge, the upper side being strongly convex. The following explanation for such differential growth suggests itself: when plants are placed in darkness there is a complete cessation of auxin production throughout the leaf. The accumulation in the larger lateral veins and more particularly in the proximal end of the midrib enables the latter to continue to elongate as long as auxin is present in optimal concentrations for growth. Little or no growth takes place in the lamina because all of the auxin has been moved into the midrib (or being present only in low con-

centrations, it is soon exhausted in intervenous portions when the plant is placed in darkness).

To test this question, heteroauxin was applied in lanolin paste to different parts of leaves after the method of Laibach (1933). There is little or no response when the paste is put on the lamina, but when applied externally to the midrib, the latter becomes sharply convex on the side where

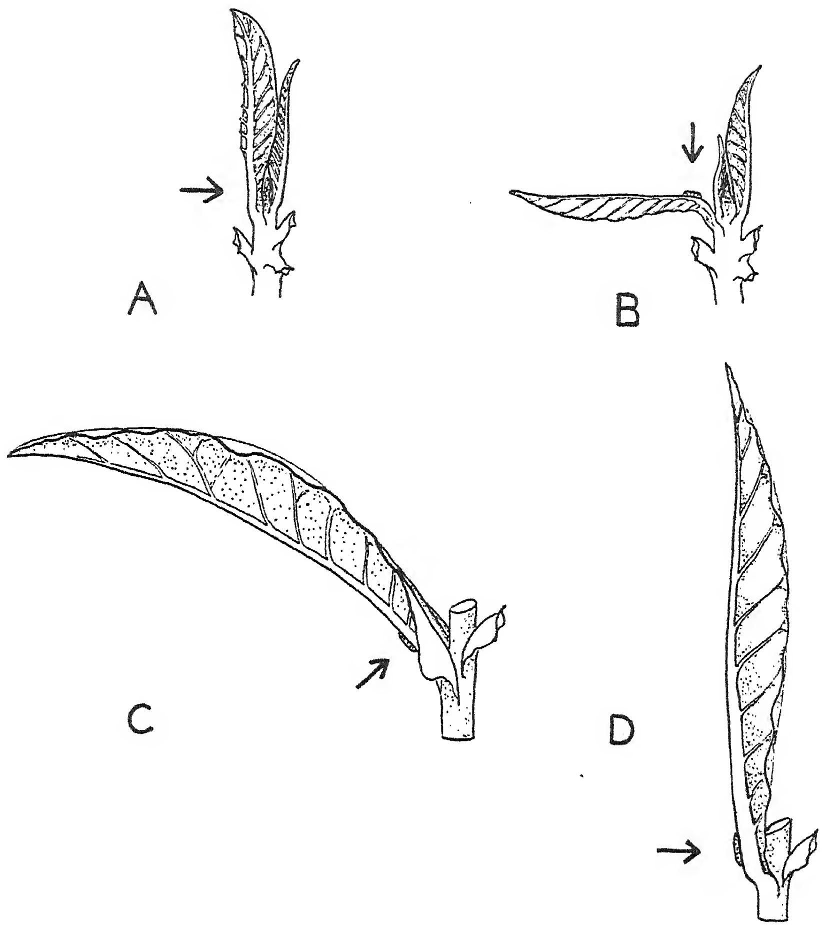


Fig. 4. Response of leaves to the application of auxin paste. A, young leaves still upright in the bud. Auxin was applied to the adaxial surface of the midrib (leaf on the left) at the level indicated by the arrow, B, same, 18 hours later. C, somewhat older leaf, on which auxin was applied to the abaxial surface of the midrib as indicated. D, same, 18 hours later. These and similar experiments were carried on in the darkroom, on plants in which the auxin was completely absent; they had been in darkness for approximately a week previous to applying the auxin.

it is applied. The bend actually occurs just below the level of application (fig. 4). The degree of response, i.e., the angle of bending, depends upon the degree of maturity of the leaf and upon the distance of the applied auxin from the proximal end. Angles up to 90° may be obtained if the paste is applied to the adaxial surface of upright young leaves at their extreme proximal end (fig. 4 A, B).

If the paste is applied to the lower (abaxial) side of the midrib at the proximal end of the leaf, the leaf will bend upward just as in the night position (fig. 4 C, D). Mature leaves do not ordinarily assume the "night" position, and so in order to determine whether age of leaf was a factor of influence, successive leaves ranging from the younger ones (starting with one 10 cm. long at the upper end of the stalk) down to mature leaves, were treated. The angle between the midrib and the internode was measured by means of a protractor before and after application. The plants had been in the dark room for 200 hours and the leaves no longer moved nor in any way changed their position from time to time with respect to the stem. The results were as follows:

LEAF NUMBER, STARTING WITH UPPERMOST LEAF TREATED	SIZE OF ORIGINAL ANGLE AT THE TIME OF TREATMENT	SIZE OF ANGLE THREE DAYS AFTER APPLICATION OF AUXIN PASTE	NUMBER OF DEGREES MOVEMENT DUE TO THE AUXIN
1	15°	0°	15°
2	35°	8°	27°
3	60°	18°	42°
4	45°	31°	14°
5	65°	10°	55°
6	40°	39°	1°
7	50°	52°	−2°

It will be noted from the table that the upper five leaves to which the auxin paste was applied showed a marked response, each leaf assuming as nearly an upright position as possible (mechanical interference with one another kept them from attaining a completely upright position). The sixth and seventh leaves which were old and becoming yellow, showed no response, a fact which falls in line with results recently reported by Mai (1934). He found that when auxin was applied to old *Coleus* petioles, they failed to react, but when applied to younger petioles they responded with greater than normal elongation.

The growth shown by midribs of younger leaves in response to the application of auxin paste indicates that the hormone is at least one of the factors responsible for growth of veins. The fact that the proximal third of the midrib is characterized by a strong *polarized growth* (fig. 1, B) and

that the auxin normally accumulates in this region, now ties up with the fact that marked growth responses take place when additional auxin is artificially applied to the midrib. That auxin paste has less effect when applied to the lateral veins may be explained by the fact that it moves rapidly into the midrib.

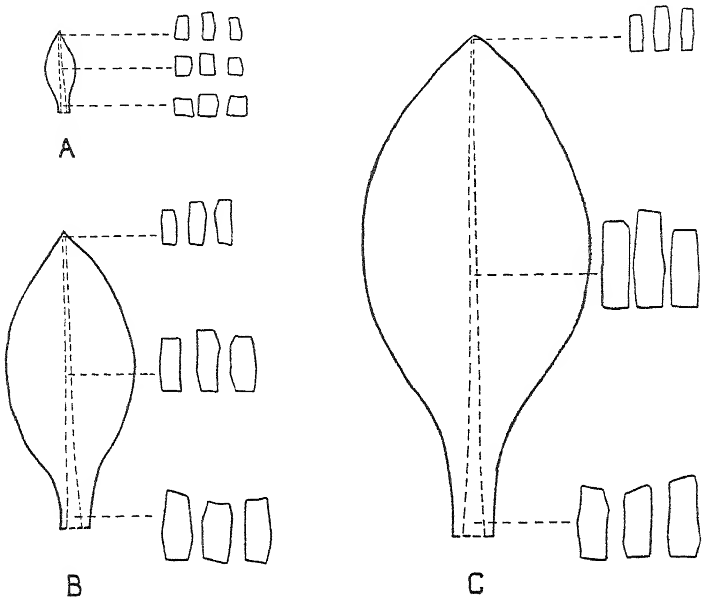


Fig. 5. Diagrams of young (A), half-grown (B) and mature (C) leaves, showing relative size of parenchyma cells in the "cortical" region of the midrib. Longitudinal sections 20 microns in thickness were made in the three zones indicated (paraffin method). Measurements of the twenty largest cells were used to compute average cell size. The range in size is indicated in the drawings. The enlargement of these cells was determined relative to the enlargement of the leaf as a whole (Huxley's "k," see text). The cells at the tip mature early. Those in the middle increase in length at about the same rate as the leaf. Those at the base increase in length about in proportion to the leaf, up to the time it is half-grown. From then on to maturity, growth is due to division and subsequent enlargement of cells; cell division in this region is correlated with a high concentration of auxin.

DOES THE AUXIN INFLUENCE CELL ELONGATION, CELL DIVISION, OR BOTH?

The distinction between phytohormones which bring about cell enlargement and those which bring about cell division was pointed out in the introduction. While it is beyond the scope of this study to discuss the question at length, an examination of increase in cell size in proportion to leaf size was made, using Huxley's formula for heterogonic growth (Avery,

1933). Data on length and volume were obtained for cells in three distinct regions in the midrib: (1) the apex, (2) middle, and (3) base of young (3 cm. long), half grown (12 cm. long), and mature leaves (30 cm. long). The twenty largest parenchyma cells were selected from the "cortical" region of the midrib at each of the three levels in the leaves of the three different ages. It was found that the cells at the tip matured early. Those in the middle increased in length at about the same rate as the leaf, throughout the period of growth. Those at the base increased in length about in proportion to the leaf as a whole, up to the time it was half grown. From then on until maturity, in this basal region, cell enlargement did not keep up with the growth of the leaf as a whole, i.e., further growth is due to division and subsequent enlargement of cells (fig. 5). Data based on increase in cell volume in proportion to leaf volume are of the same order as the above for cells in the middle of the leaf. At the base, cell volume is increasing only 0.3 to 0.4 times as rapidly as the volume of the leaf as a whole, which corroborates the above evidence for cell division. New cells, therefore, are being added in the direction of polarized growth. It is difficult to interpret the data. The hormone may be promoting cell division. It may on the contrary be promoting cell enlargement, and the cells after reaching a certain size, divide and thus maintain a favorable nuclear-cytoplasmic ratio. In either case, there seems to be a definite relation of the auxin to polarized growth.

It is impossible at this time to say precisely what relationship exists between auxin and *localized* growth in various portions of the *Nicotiana* leaf.

THE HORMONE PRESENT IS PROBABLY AUXIN *A*

Since (Kögl and others) auxin *a* is stable in the presence of acid and auxin *b* is sensitive to both acid and alkali, and heteroauxin is stable to alkali but destroyed by acid, it seems likely that auxin *a* is the hormone present in *Nicotiana* leaves, because in numerous experiments it was extracted with acidulated chloroform.

SUMMARY

1. A hormone, probably auxin *a*, is demonstrated in growing leaves of *Nicotiana*. The concentration is roughly inversely proportional to the age of the leaf, that is, it is present in greater concentration in young leaves and tends to disappear as a leaf matures.

2. There is a definite auxin concentration gradient from tip to base of leaf. It is low at the distal end, and successively higher toward the base.

3. Auxin is produced in nearly equal concentrations over the entire

lamina in young rapidly growing leaves, and the gradient referred to in "2" is due to accumulation at the base.

4. Accumulation and transport of auxin take place mainly in the midrib, to which the auxin is conveyed by the large lateral veins.

5. Movement of auxin in the leaf is polar, i.e., transport takes place only from tip toward base of leaf, and from lateral veins into the midrib.

6. Auxin tends to disappear as the leaf approaches maturity, first at the apex and then gradually toward the base.

7. The formation of auxin in the leaf depends upon the presence of light.

8. Elongation of the midrib and probably the larger lateral veins is due to favorable concentrations of auxin. Growth can be induced by external application of the auxin paste to the midrib. Similar applications to the interv nous regions or lateral veins have little effect, probably because the auxin is moved rapidly to the midrib. This suggests that the impetus for leaf development may come from the midrib and main lateral veins, due to the accumulation of auxin in them.

9. Auxin is partly responsible for the growth pattern shown by the leaf: the proximal portion of the midrib (and therefore of the entire proximal end of the leaf), where auxin accumulates, undergoes relatively greater growth in length ("polarized growth") than the leaf as a whole.

Cell division is shown to be taking place in the proximal end of the midrib, where the auxin accumulates. This is contrary to the present generally accepted notion that auxins influence only cell enlargement. Auxins and their possible influence on cell division and cell enlargement are discussed briefly.

It is a pleasure to express my appreciation to Dr. F. W. Went, at whose invitation I visited the Kerckhoff Laboratories at the California Institute of Technology in the summer of 1934. With similar appreciation I wish to convey my thanks to Dr. K. V. Thimann, Mr. Folke Skoog and Mrs. Franz Dolk, for their assistance and helpful discussions.

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The natural distribution of Cytisus scoparius in Virginia with special reference to soil reaction[1]

Thomas W. Turner

INTRODUCTION

While studying the flora in certain sections of tide-water Virginia, my attention has been directed frequently to *Cytisus scoparius*, or Scotch broom as it is generally known. Its localized distribution and the apparent indifference as to kind of soil in which it is seen to grow, prompted me to make some studies for the purpose of determining the extent of its distribution over the state and at the same time to investigate the reaction of the soil from which the roots take their nutrients. The absence of seedling growth, in and around places of luxuriant adult stands, and the almost weedy appearance of the same in other places not far removed from these stands, have led to experiments, also, to determine to what extent germination of seeds is influenced by the hydrogen ion concentration, and to show further whether or not the germination of the seeds requires a soil reaction different from that in which roots are found growing most abundantly.

Attention is further called to this plant because of the showy yellow flowers, which in massed aggregations, present a beautiful scene along the roadside in late spring and give much promise from the point of view of the nurseryman and florist.

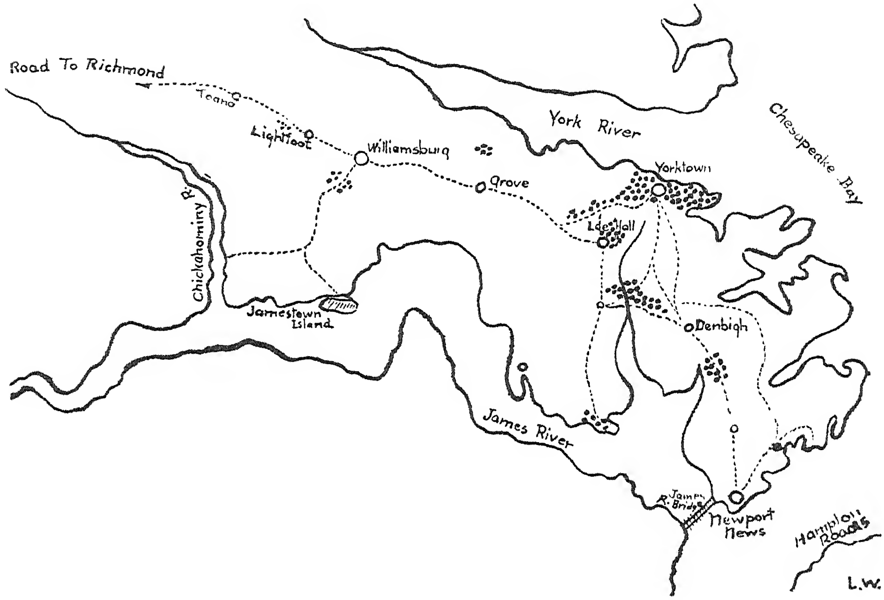
It was in 1884 that a French landscape gardener by the name of André noted a seedling differing from the surrounding *Cytisus* plants in having crimson wing petals; he selected this and from its propagation have been derived, chiefly through efforts of European gardeners, several well known commercial varieties. American ornamental plant growers have given but little attention to the common variety of broom which has become naturalized in several restricted localities in different parts of the country. It has many commendable natural features, among which may be mentioned the abundant floriferous habit, extending over a rather long period, the large bright yellow flowers which are very attractive against a background of dark green twigs and foliage, the comparative hardiness and ease of propagation from seeds, as well as from cuttings.

DISTRIBUTION AND LITERATURE

While *Cytisus* is a well known wild plant, sometimes considered a troublesome weed, in Great Britain and parts of the continent of Europe,

[1] Contribution from the Department of Biology, Hampton Institute, with cooperation of the Virginia Academy of Sciences, Richmond, Va.

it has become established in the United States and Canada slowly and only along or near the coast line. This is true of the Pacific as well as the Atlantic Coast. Gray's *New Manual* lists it as occurring on "sandy barrens, etc., Nova Scotia; south-east, from Massachusetts to Virginia and southward." Britton and Brown's *Flora* gives the distribution as follows: "In waste places, Nova Scotia to Massachusetts, Delaware and Virginia, also in California and on Vancouver Island." It might be added that along the Pacific Coast it is to be found in the States of Oregon and Washington as well as California.



Map of the Peninsula Section of Virginia. The distribution of *Cytisus scoparius* over the Virginia Peninsula.
Broken lines—auto roads
Dots—*C. scoparius*

The Virginia distribution, with which this study deals, is quite typical of the general distribution as we see it on this side of the Atlantic. There is no extensive nor gradual invasion of new areas at any place. Thus, it would seem that the dotted growths as shown on the map, the abrupt mature patches, observed in places, and the springing up of seedlings in certain areas recently burnt over and cleared of trees, cannot be explained in a simple manner. There are certain barriers to the distribution of this plant which probably deserve more attention than has been given to them heretofore.

The plant is decidedly heliophilous and, in the Peninsular area, tends to cling near the roadside, the explanation of which is obvious since frequent cultivation of the cleared places serves to eliminate it before it has time to make a stand.

There is much speculation as to the origin of seeds giving rise to the first local invasions; the prevailing tradition attributes it to seeds in the horse feed and bedding imported during the Revolutionary Campaign about Yorktown. A further tradition is that the Campbell, Albemarle, and Bedford County growths originated in seeds brought from Europe and planted by Thomas Jefferson. The distinguished Virginian maintained homes in the latter two counties.

The soil reaction of *Cytisus* has been studied by Professor E. T. Wherry of the University of Pennsylvania. He places it in a group, having a pH ranging from 5 to 6.5. As my observation showed it to be growing rather freely on stiff red clay banks along the side of the roads as well as in the more usual sandy loam, a check up on the root soil reaction was deemed advisable. Such was later undertaken, though not yet completed, for germination of the *seeds* also.

It should be said here that the extreme western part of the state has not been visited in the study; thus reservation is to be made for any omission concerning this section.

METHOD AND RESULT

In checking up the localities of naturalized invasions of broom, I have had the helpful assistance of the Federal Farm and Home Demonstration agents in the several counties of the state, who pointed out any growths known to them. These localities were then followed up for personal observation and study. Samples of soil were taken from the shallow roots which usually are found most abundant from one to three inches below the surface. These samples were carried to the laboratory in cleaned, stoppered bottles, sometimes in manila bags, for the determinations. The number of samples taken from the different areas vary as shown in the table on the following page.

Careful pH determinations were made of about 200 samples of soils collected sometimes from as many as fourteen different patches in a particular locality covering the four Peninsular counties. Determinations were also made of samples from other parts of the State (Campbell, Bedford, Prince Edward, and Amelia Counties) in which broom has been found growing luxuriantly in a wild state.

The soil was extracted by using one part to four of distilled water and

pH value of soil around nutritive roots of Cytisus scoparius

SAMPLE	TRIP 1		TRIP 2		TRIP 3		TRIP 4		TRIP 5		TRIP 6		TRIP 7		TRIP 8		TRIP 9	
	SOIL	pH	SOIL	pH	SOIL	pH	SOIL	pH	SOIL	pH	SOIL	pH	SOIL	pH	SOIL	pH	SOIL	pH
1	SaL	6.2	L	5.8	C	6.0	*	6.8	SaL	7.2	SaL	6.8	Sa	6.2	*		L	6.2
2	SaL	5.8	L	6.0	C	6.2		6.8	SaL	7.2	SaC	6.3	C	6.3			L	6.2
3	SaL	6.2	C	6.5	C	6.2		6.8	SiL	6.2	SiC	6.7	L	6.5			CL	6.2
4	SaL	6.8	C	6.4	CL	6.2		6.8	SiL	5.9	L	6.5	SiL	6.5			L	6.0
5	SaL	6.6	Si	6.3	CL	6.4		6.8	L	6.0	Sa	6.5	SaC	6.4			L	6.2
6	SaL	6.6	SiC	6.3	CL	6.4		6.0	L	6.6	Sa	6.7	SaC	6.7			SaC	6.2
7	SaL	6.6	SaL	6.3	CL	6.4		6.6	C	8.2	L	6.7	SaC	6.0		6.0		
8	SaL	6.4	SaL	6.3	CL	6.6		6.6	C	8.3	L	6.8	SaC	6.2				
9	SaL	6.4			CL	6.6		6.8	Sa	6.7	SaC	6.4	SaL	6.1				
10	SaL	6.4			CL	6.6		6.8	SaL	6.2	SaC	6.5	SaL	6.8				
11	SaL	6.4			CL	6.6		6.0	CSa	6.3	SiC	6.4	SaL	6.8				
12	SaL	6.2			C	6.2		6.0	CSa	6.2	SaC	6.5	Sa	6.6				
13					C	6.0		6.0	CGr	6.6	SaL	6.6	C	6.7				
14					C	6.0			CGr	6.6	SaC	6.4	L	6.5				
	Averages	6.4		6.2		6.3		6.6		6.7		6.6		6.5		6.0		6.2

Legend: C—Clay; Gr—Gravel; L—Loam; Sa—Sand; Si—Silt.
* Not recorded.

shaking vigorously. The aqueous mixture was allowed to stand, for clearing and settling of soil particles, usually five to twelve hours. The determinations were made, for the most part, by the colorimetric method, using the La Motte Testing Set Model B for the same. As a check upon these results, however, a quinhydrone electrode apparatus was used on a few random samples.

The results of the soil determinations (colorimetric method) are given in the table. This table shows a set of samples, as many as fourteen in some cases from each patch, taken from all the patches of naturalized growths found in the Peninsular section and five from areas much farther inland. No attempt is made here to present a minute and technical description of the soil. The simple classification used is based upon Emerson's *Principles of Soil Technology*. The pH values of the samples from the different areas of the nine localities are presented in the table with averages of the same. Attention should be called, however, to two samples (7 and 8 in trip 5) of clay with pH values of 8.2 and 8.3. The plants appeared normal in this highly alkaline soil. It is possible that the roots from which the soil was removed were not those functioning chiefly in the nutrition of the plants. Checking up determinations made with the quinhydrone electrode apparatus, showed a range that was in general quite

similar in pH (ranging from 6.00 to 6.7) to the colorimetric. For the electrometric measurements certain random selections were made from samples whose pH had been determined first by the color method. As shown in the table, samples 4, 5, and 6 of trip 1 gave pH values 6.8, 6.6 and 6.6; for these same samples electrometric measurements gave 6.05, 6.00 and 6.4 respectively. Trip 4, sample 4 gave, on the colorimetric basis, a pH of 5.9, the electrometric measurement gave the same figure (5.9). For the, apparently, abnormal sample 7, trip 5, the color measurement was 8.2, the electrometric measurement for this was likewise 8.2.

DISCUSSION AND CONCLUSION

Dr. Wherry lists this plant among those preferring a subacid soil—pH 5 to pH 6—growing also in mediacid soil having a mid value of pH 4.5 to what he designates a high miniacid soil with a mid value of pH 6.5. It would seem from the soil tests made during the present study that its pH tolerance range is much narrower than Dr. Wherry's list would indicate and its acid preference much less pronounced. Instead of having a range from 4.5 to 6.5 it appears to show a decided preference of a range from about 6 to 6.7.

To what extent the narrower range found becomes a limiting factor in the distribution of the plant cannot be determined with any definiteness from the facts in hand, but certainly in presence of such range its slow natural distribution would be expected wherever a widely varying soil reaction is encountered. A comparison of the reaction of nearby soils which had remained untilled for some time was not made but might have been instructive.

Cultivation practices must also be taken into consideration as a limiting factor of no small importance in the areas under discussion. Thus, when these two factors are judged in connection with a reduced chlorophyllous mechanism that makes *Cytisus* seek the open places, we may get some clue as to its peculiar distribution.

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A mislaid mistletoe

WILLIAM TRELEASE

In February, 1934, my long-time friend, Professor C. Conzatti, of Oaxaca, sent me specimens of a *Phoradendron* collected by him and a colleague in June, 1906, and again in March, 1909, by himself and one of his sons, both in the mountains of the Mexican State bearing the same name.

Both specimens were labeled *P. auriculatum*, a manuscript name that I must have furnished in some way while preparing my monograph of the genus *Phoradendron*. This binomial, without indication of author, appears in the list of species excluded from the genus (p. 217); but, unlike other excluded species—with a single exception, without indication of an accepted name, and it appears also in the index to specific names with a quaere as to its application (p. 219).

Professor Conzatti's curiosity as to where I had seen and so labeled the plant, was fully equaled by my own, coupled with wonder concerning its disappearance except as an excluded name from a monograph published nearly a decade after it had been collected first. No specimens occurring in my own collection, an appeal was made to the Missouri Botanical Garden, where all of my earlier material is deposited; and, no trace of it being found there, to the United States National Herbarium, in which the genus had been studied, but where nothing of the kind occurs.

Preoccupation with other matters, and a rather prolonged vacation in the summer, prevented me from making further search for the missing species until recently.

A more thorough search now reveals the fact that I first encountered it in the Gray Herbarium, probably on my return from Europe early in 1913, at which time the appended manuscript description was drawn up under the questionable name. When my notes were arranged in monographic form, two or three years later, though *P. auriculatum* found its way into the index without being placed and for this reason into the list of excluded names, the description drifted out of sight. Now that it has come to light again, the reason for its exclusion appears to have been a doubt as to the availability of the proposed name, and neglect either to clear it of suspicion or replace it by an acceptable name before the monograph was published. The seeming difficulty of that time not being evident to me at present, the really attractive species is now given belated publication, with apologies to its talented discoverer.

Phoradendron auriculatum n. sp.

(Aequatoriales Amplectentes)

Somewhat pseudo-dichotomous; dioecious?; smooth and varnished, with sharply 2- or 4-angled internodes. Cataphyls confined to the lowest joint, solitary, basal, tubular; leaves subelliptical, 20–30×50–90 mm., sessile and auriculate, obtuse, sometimes slightly mucronate, rosy-margined, thick, prominently 7–9-nerved from the base but scarcely veiny. Spikes mostly

clustered, rather long (becoming 50–60 mm.) with about 4 fusiform joints some 30-flowered in 6 ranks; peduncle stout, scarcely 5 mm. long; scales spreading truncate, scarcely ciliate; immature fruit slightly cellular-papillate, globose, 3 mm. in diameter, with closely inflexed sepals.

Cordilleran region of Mexico; Cerro Nueve Puntas, Chiconahiultepec, Matatlan (Conzatti and Vasquez 1511). El Parian, Etla (Conzatti and Son 2378).

Atractobasidium, a new genus of the Tremellaceae

G. W. Martin

(WITH TWO FIGURES)

The fungus which is the subject of this note was collected by C. L. Smith in Mexico some time during the years 1894 to 1896. It has been in the collection of the State University of Iowa under the name *Corticium nigrescens* Fries, as No. 98 of a miscellaneous series of collections supplemental to Smith's Central American Fungi. So far as known it was not distributed and I assume that our material, which fortunately is ample, represents all that was gathered.

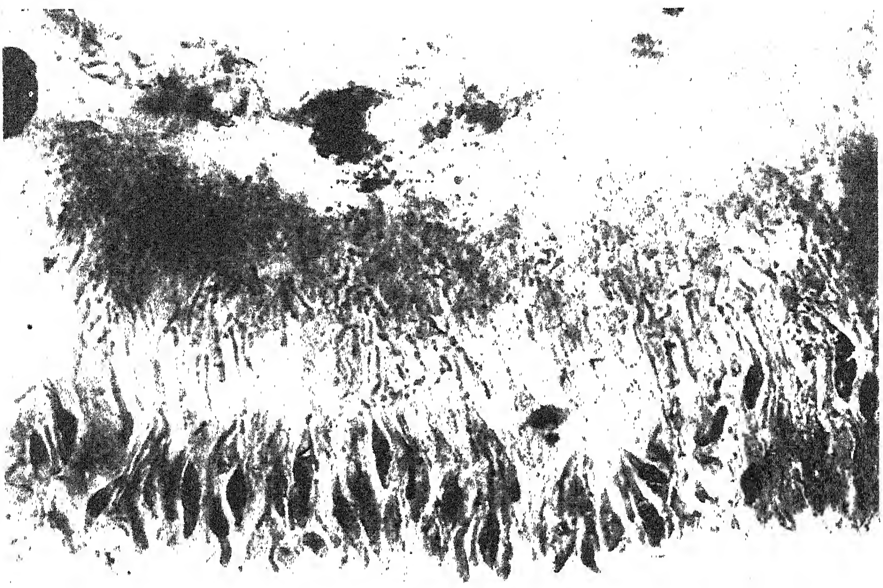

Fig. 1. Photomicrograph of freehand transverse section of fructification, stained with phloxine, ×450.

Examination of the hymenium (fig. 1) shows at once that the fungus is not a *Corticium* but a heterobasidiomycete with basidia of a type not hitherto reported, somewhat intermediate between those of the *Tremellaceae* and those of the *Auriculariaceae*. It is quite impossible to include it in any previously recognized genus and a new genus must therefore be established to accommodate it.

Atractobasidium gen. nov.[1] (*ἄτρακτος*, a spindle).

Resupinate, waxy, drying horny: basidia at first clavate, then fusiform, finally divided into four cells by oblique-transverse septa, the two later septa at right angles to the first.

Atractobasidium corticioides sp. nov.[2]

Receptacle broadly effused, attaining 10 cm. or more in length and 3 cm. or more in width, thin, adnate, waxy, drying horny, the central portion benzo brown*[3] to Quaker drab* when dry, becoming army brown* when soaked, fading to sordid white at the thin, indeterminate margin; in section 150–300μ thick, consisting of a thin, brownish basal layer about 20μ thick, then a densely interwoven central portion composed of colorless, irregular, vesiculose and submoniliform hyphae intermingled with some brownish strands, the two layers occupying from slightly more than one-half to two-thirds the thickness of the fructification, the remainder being occupied by the hymenium, composed of closely packed, vertically arranged basidia and slender, unbranched paraphyses with tortuous, submoniliform tips, the whole immersed in a gelatinous matrix which forms a continuous layer over the surface, the entire section with rather large, subcrystalline, calcareous accretions scattered sparsely throughout; basidia at first clavate, then fusiform, $33–45 \times 8.5–12.5\mu$, eventually four-celled; divided first by a transverse-oblique septum into two cells, each cell again divided by an oblique septum at right angles to the first; each of the four cells so formed producing a tortuous epibasidium of approximately uniform diameter except toward the tip, where it is often somewhat inflated, $30–40 \times 2–3\mu$, tipped by a sterigma and a spore; basidiospores ovate-cylindrical to allantoid, $11–13.5 \times 4.5–6\mu$.

Type: Jalapa, Vera Cruz, Mexico, 1894–1896, *C. L. Smith* 213. The type specimen is in the herbarium of the State University of Iowa, with portions distributed to the Farlow Herbarium, the New York Botanical Garden, the Missouri Botanical Garden and the United States National Herbarium.

The original material is in a number of fragments, but when these are pieced together it becomes evident that the dimensions given in the de-

[1] Resupinatum, ceraceum, siccatum corneum; basidia primum clavata, deinde fusiformia, septata, septo primo oblique transverso, septis secundis rectis angulis primo septo adhaerentibus.

[2] Receptaculum late effusum, ceraceum, siccatum corneum, fuscum, margine pallidum; basidia fusiformia, 3-septata, septo primo oblique transverso, septis secundis rectis angulis primo septo adhaerentibus, $33–45 \times 8.5–12.5\mu$; epibasidia filiformia, $30–40 \times 2–3\mu$; sporae ovato-cylindraceae vel allantoideae, $11–13.5 \times 4.5–6\mu$.

[3] An asterisk affixed to names of colors indicates that they are used in the sense of Ridgway, Color Standards and Nomenclature.

scription are conservative. Judging by analogy with forms of similar habit, its growth may well be much more extensive. While the general appearance is that of a *Corticium*, the texture is unlike that of any *Corticium* with which I am familiar. The basidia, of course, constitute the striking characteristic. At first nearly cylindrical (fig. 2i), when they have attained full

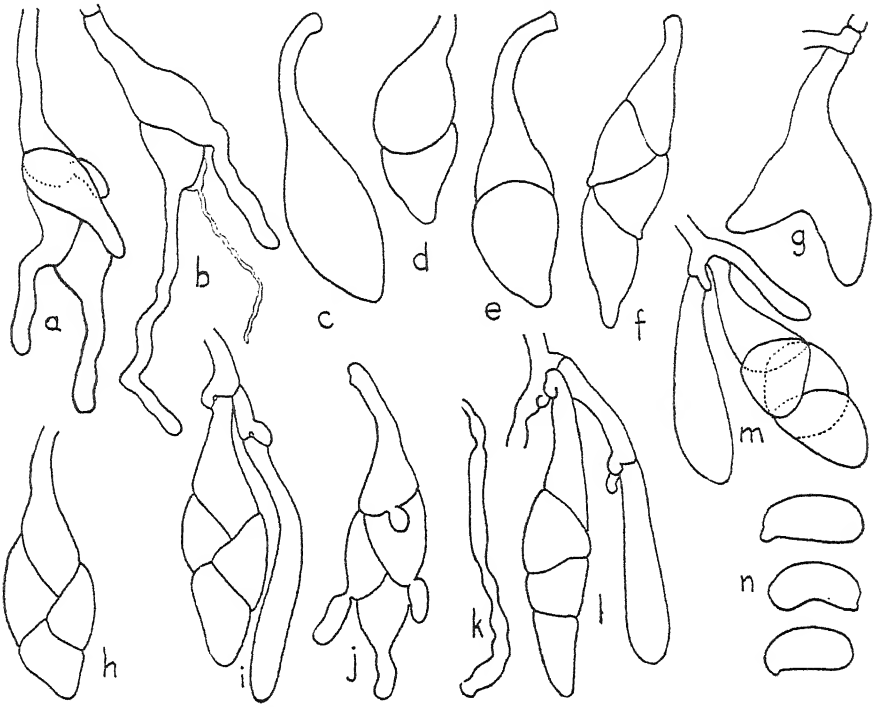

Fig. 2. Drawings made with aid of camera lucida, reduced in reproduction to ×1000. a, j. Basidia with four partially developed epibasidia. b. Basidium with two cells bearing epibasidia, one cell collapsed, fourth cell not visible. c. Mature probasidium. d, e. First division completed. f, h. Four-celled basidia, epibasidia beginning to develop in f. g. Basidium of unusual shape. i. Probasidium and four-celled basidium, showing clamp connections. k. Paraphysis. l. Probasidium and four-celled basidium, the latter with secondary walls not reaching the first septum. m. Two probasidia and fully divided basidium in cluster. n. Three spores.

size they are clavate-fusiform (fig. 2c), then, at about the time the first division occurs, the distal end becomes bluntly pointed and often somewhat attenuate (fig. 2d, e). The first division is obliquely transverse, at an angle of about 45° to the axis of the basidium, the second divisions are at right angles to the first, but on account of the shape of the basidium the secondary walls do not meet on opposite sides of the first septum, as in typical basidia of the tremellaceous type (fig. 2h, i). The second divisions must follow the first division very promptly since unseptate and four-celled

basidia are much more abundant than those with two cells. Most of the basidia are provided with prominent clamp connections at the base (fig. 2i, l, m). A few of irregular form were found (fig. 2g) but these seemed to be no more abundant than is usual in tremellaceous fungi.

The position of the first septum recalls the situation in *Sirobasidium*. The resemblance is, however, superficial only. In *Sirobasidium* the oblique position of the septum is clearly an adaptation to the catenulate arrangement of the basidia. Lagerheim and Patouillard (1892) illustrate the septa in the terminal basidium of both species they describe as strictly longitudinal, and this seems to be the case with all the basidia in the chain shown in their fig. 1f. The secondary septa are shown on opposite sides of the primary septum, as in *Tremella* and *Exidia*. The basidia of *Sirobasidium* as pictured by Möller (1895, pl. 6) and by Coker (1920, pl. 55, figs. 1, 2; 1928, pl. 47, figs. 1–4) are never more than 1-septate, and the septum in the terminal basidium is usually oblique, but occasionally longitudinal or directly transverse. Furthermore, the basidial segments of *Sirobasidium* do not produce epibasidia, but bear the basidiospores directly These differences, wholly aside from the catenulate arrangement of the *Sirobasidium* basidia and the gross habit and morphology of *Atractobasidium*, make it clear that the latter genus cannot be accommodated in the *Sirobasidiaceae*. The resemblance to certain genera of the *Auriculariaceae* with swollen, clavate, transversely septate basidia is also suggestive at first sight. One exceptionally slender basidium was observed in which the secondary septa had failed to reach the first septum (fig. 2l). Such irregularities are of common occurrence in the *Tremellales* and have been illustrated many times. An example of an irregular basidium of *Tremella lutescens* suggesting the regular type in *Atractobasidium* is shown by Coker (1920, pl. 57, fig. 4). Nevertheless, the regular, perpendicular alignment of the second basidial septa with reference to the first septum is held to exclude the genus from the *Auriculariaceae* and to establish its position in the *Tremellaceae*. It remains true, however, that the *Atractobasidium* type of basidium is more like basidia such as those of *Platygloea* and *Auricularia* than any of the tremellaceous basidia heretofore described. Rogers (1934) has recently suggested the possible independent derivation of the auriculariaceous basidium from the primitive tulasnellaceous type, or even from an hypothetical ascomycetous ancestral group. The existence of *Atractobasidium*, however, suggests possible direct relationship between the *Tremellaceae*, through that genus, with the two genera of the *Auriculariaceae* mentioned.

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Nuclear behavior in the tapetum of Hosta caerulea, with special reference to the divisions[1]

Wm. E. Roever

(with plates 19 and 20)

INTRODUCTION

Mitosis is commonly defined as nuclear division involving the formation of chromosomes, while amitosis is regarded as division of the nucleus in a "resting" condition, that is, without the organization of chromosomes. It was once believed that amitosis was the prevalent method in cell division and mitosis, the unusual type; but as work on nuclear division accumulated in all fields of biology, it became evident that the converse was true. Promulgation of the chromosome theory induced the continued and critical study of nuclear division in both plant and animal kingdoms. With the gradual accumulation of data, mitosis steadily encroached upon domains where amitosis was formerly thought to be the routine method of nuclear multiplication, so that at present few examples remain to be pointed out as bona fide instances of nuclear fission. In any case, it is extremely doubtful whether there exists a single case of amitosis in the sense of a division having the same reproductive potentialities as ordinary mitosis.

In reference to the problem in protozoa, Kofoid (1923) says, "Amitosis as described in protozoa is either a pathological or degenerative process as it is in metazoa." Among fungi, the budding of yeast, long regarded as a classic example of amitosis, has been distinctly figured and described as a case of mitosis (Kater, 1927); and in the higher plants described instances of nuclear fission have, in general, occurred in degenerative or pathological tissues, or have been found to be due to incomplete mitosis or fusion.

Among the plant tissues that have received much study in connection with this problem of nuclear division has been the staminal tapetum. Conflicting reports concerning the methods of division in the tapetum suggested an investigation of nuclear behavior during the development of this nutritive layer.

The tapetal cells in the anthers of most pteridophytes and spermatophytes are characterized by a multinucleate condition that appears early in the development of the pollen sacs. The origination of this multinucleate phase has variously been described as either mitotic or amitotic, and one author reported that both methods of division occur.

[1] Submitted in partial fulfilment of the requirements for the degree of Master of Science in Rutgers University.

After the polynucleate stage has been attained the tapetal layer undergoes changes which are closely correlated with microsporocyte development. Such changes are markedly evident in the behavior and appearance of the nuclei and culminate in tapetal degeneration coincident with the formation of pollen.

HISTORICAL

The following investigators record mitosis in tapetal cells: Strasburger (1882), Bonnet (1912), Gates and Rees (1921), Campin (1925), Mascré and Thomas (1930), Thomas (1931), Steil (1933), Cooper (1933) and Smith (1933). On the other hand, Tischler (1906) speaks of both mitosis and amitosis in the tapetum of certain *Ribes* hybrids. O'Neal (1920) records amitosis in the same tissue of *Datura Stramonium.* Meyer (1925) speaks of polyploid tapetal nuclei that arise by splitting of chromosomes without loss of the nuclear membrane. Conard (1926, 1928), in wound tissue of *Tradescantia* stems, describes amitosis followed by reunion of the amitotic segments and subsequent division of the nucleus by mitosis.

As for animals, Macklin (1916) records amitosis in the living tissue of the embryo chick but Lewis and Lewis (1924) believe that most, if not all, amitosis in tissue culture has been observed in degenerative or pathological material. That artificial fission of a nucleus can be followed by reunion of the parts and subsequent mitotic division of the reformed nucleus is shown by Chambers (1917). Conklin (1917), in cleavage divisions of *Crepidula plana,* records only anomalous mitoses simulating nuclear fission.

MATERIALS AND METHODS

Buds of *Hosta caerulea* Tratt. in all stages of development were taken from plants growing in the vicinity of New Brunswick, New Jersey. The material used in this study was collected in the latter part of June, and for the most part, very young buds were found to give the required stages.

In fixation tips of buds were cut off to allow quicker penetration of the anthers, and air was always exhausted, as the material did not readily sink in the fixing fluids because of air entrapped in the buds. Various fixing agents were tried such as Carnoy's fluid, chrom-osmic-acetic, and Allen's modification of Bouin's fluid "PFA_3." Only the last gave satisfactory results. It was found that the action of Carnoy's was too rigorous and induced excessive plasmolysis. Chrom-osmic-acetic fixatives, on the other hand, caused the densely cytoplasmic tapetum to appear too opaque for satisfactory observation, and the opaqueness was found to persist after subjecting the sections to a thirty-three per cent solution of hydrogen peroxide in seventy per cent alcohol for as much as twenty-four hours.

In "PFA_3," material was fixed for twenty-four hours and washed the same length of time. Smear preparations were then made in an effort to find some relation between bud size and microsporocyte development. Belling's aceto-carmine method gave excellent results. The stain was prepared by boiling an excess of powdered carmine in forty-five per cent glacial acetic acid. Anthers were then teased apart with a pair of steel needles and mounted in this solution. The various stages in pollen mother cell development were thus obtained and correlated with bud size. This approximate correlation proved to be of value in selecting buds for sectioning with the view of obtaining specific stages in microsporocyte development.

In the preparation of sections the paraffin method was employed. Both transverse and longitudinal sections of the buds were cut, but the latter proved by far the most useful. Most ribbons were cut at five microns and sections were mounted serially. In staining, Heidenhain's iron-alum haematoxylin was used, and in some cases a light counter stain of orange G, in clove oil, was applied.

OBSERVATIONS

The resting nucleus

At the primary sporogenous stage of an anther its wall consists of four layers, the epidermis, the immature endothecium, a transition layer, and the tapetum adjoining the primary sporogenous tissue. The young tapetal cells are square or oblong in outline, but as the anther enlarges, growth stresses force them into various angular forms. The nuclei are slightly hyperchromatic, but as the tapetum develops they become increasingly rich in chromatin.

When the microsporocytes are in the resting stage the tapetal cells are very small as compared to their size at maturity, and the single large nucleus occupies about half a cell. At this period the appearance of the resting nuclei is quite distinct. In general, they are spherical to oval in shape and contain from one to several hyaline vesicles each of which has a prominent, densely staining nucleolus. When a single vesicle is present it occupies a large part of the nucleus and contains a large nucleolus (fig. 1). If more than one is present, the vesicles are correspondingly smaller and have less prominent nucleoli (figs. 12a, 12b). Careful focussing reveals several fine supporting strands running from the periphery of a vesicle to its nucleolus (fig. 1). If the nucleoli are small these strands are not easily detected. Slight accumulations of chromatin are seen bordering the vesicular region, these being especially noticeable where two vesicles are ap-

pressed. The remaining chromatin of the resting nucleus forms a thin reticulum lining the nuclear membrane.

The foregoing description is also characteristic of the tapetal nuclei during the synizetic stages of the pollen mother cells. While synizesis is in progress the first mitotic divisions begin in the nutritive layer.

As the anther develops the tapetal nuclei gradually undergo a considerable change, and by the time the pollen mother cells have reached the open spireme stage the nuclei are decidedly more hyperchromatic than during the earlier periods of growth. Most of the tapetal cells have at least doubled their earlier dimensions and the nuclei have enlarged correspondingly (fig. 3). As a result of the first mitotic division many of the cells are binucleate; some are uninucleate because the division was incomplete or because it was accompanied by cytokinesis, while others may be uninucleate because the first division has been delayed. The large resting nuclei have, for the most part, lost the nicely rounded or oval shapes that characterize them during and before synizesis. Nuclei resulting from incomplete first divisions are often dumb-bell-shaped or U-shaped (figs. 11a, 11b, 11c), and where a pair of nuclei are present, they, too, frequently have irregular outlines.

The internal condition of the nuclei is also considerably modified. Instead of the few prominent hyaline vesicles of earlier stages one finds smaller but more numerous vesicles (fig. 11c); as a rule ten or more are present. These are often considerably masked by the chromatin content of the nuclei. In favorable cases, tiny spheres of chromatin (chromocenters) are seen attached along the nuclear reticulum (figs. 3, 11b). The whole organization of the nuclei is considerably obscured by flocculent and granular accumulations of chromatin along the nuclear reticulum. By and large, the irregular and glutted appearance of the nuclei, even at this early stage of development, gives the impression of a lack of physiological control. The condition is comparable to what is observed in many pathological or degenerative tissues. That functional activity is affected is shown by the mitotic irregularities that are prevalent. These will be described presently. The appearance suggesting functional disability of the nuclei becomes evident coincident with the rapid increase in size of the tapetal cells, and seems to be correlated with the accumulation of nutritives to be used in pollen maturation. This appearance of the resting nuclei, which becomes evident at the spireme period of the microsporocytes, remains essentially the same until tapetal degeneration which, in normal anthers, occurs about the time of tetrad formation. Such changes as do take place merely emphasize conditions that have already manifested themselves during the spireme stage.

Although breakdown of the tapetal cells usually occurs shortly after the tetrads are formed this is not always true. In some instances a premature degeneration is found as early as the spireme stage of the pollen mother cells; this may take place in a portion of a locellus only. Such breakdown always includes the microsporocytes in the affected locellus or portion of a locellus. A mechanical or physiological injury is apparently involved. In these cases of early degeneration the behavior of the tapetal nuclei is quite constant. Resting nuclei stain as dense, black spheres having a granular surface (pyknosis) (fig. 4); these finally fragment into globules of various sizes (fig. 5) and disappear (dissolve?). Other nuclei are caught in various stages of division; they, too, stain heavily and ultimately disappear by a similar fragmentation as in the preceding case.

In normally developing anthers tapetal breakdown usually begins shortly after tetrad formation. Vacuoles form at two opposite ends of a tapetal cell and gradually enlarge. The cytoplasm begins to take the haematoxylin stain to a slight degree; but the nuclei do not stain as heavily as in earlier periods of growth; they become vacuolate and their boundaries reach a maximum of irregularity characterized by lobations and ragged edges (fig. 30). Growth of the microspores rapidly crushes the tapetal cells and releases the nutritive fluid which flows into the locellar cavity where it is seen as a pale yellow substance surrounding the microspores. The crushed tapetal layer appears as an irregular black line in which an occasional dark nuclear mass is to be distinguished. Some locelli contain sterile pollen only. In these, the tapetal cells persist beyond the normal time because the microspores do not enlarge; consequently the tapetum is not crushed, and no tapetal fluid is to be found in the locellar cavities.

The nuclear divisions

All observed cases of nuclear division in the tapetum of *Hosta caerulea* were mitotic. Amitotic appearances are readily explained on the basis of aberrant mitoses, vesicular appearances of nuclei, close appression of two nuclei, or degenerative fusions. Cytokinesis does not typically accompany divisions of tapetal nuclei and the cells are consequently multinucleate. Occasionally cytokinesis does occur, and wall formation may be either anticlinal or periclinal; if the former, it increases the size of the locellus; if the latter, the tapetum becomes two cells in thickness at the point of division. Mitoses occurring within a given multinucleate cell are always simultaneous (figs. 18, 25, 26).

During the resting stage of the microspore mother cells the tapetal cells are uninucleate and no mitotic figures are to be seen. At this time the vesicular nature of the nuclei frequently simulates amitosis or fusion

(figs. 12a, 12b). But with the beginning of synizesis the first mitotic divisions of the tapetal nuclei become evident, and by the time maximum synizetic contraction is reached many of the cells are binucleate or the first division is in progress (figs. 2, 8). When division is normal the daughter nuclei nearly always become closely appressed (fig. 6). Each of these appressed nuclei clearly maintains its identity, and no fusion is observed while the nuclei are in the resting stage.

At times the first mitosis is incomplete and a chromosome bridge is left connecting the daughter telophase groups (fig. 7); the resulting nucleus is presumably tetraploid (figs. 3, 7, 9, 10, 11a, 11b, 11c) and often presents an organization easily misinterpreted as the result of fusion or amitosis; dumb-bell-shaped or U-shaped nuclei are the commonly formed types. Tripolar spindles are seen occasionally (fig. 23). The exact distribution of chromosomes in such cases is problematical and can only be estimated by the size of the daughter chromosome groups, for the clumping of chromosomes that occurs in the tapetum makes accurate counting impracticable. At any rate, such division involves the apportionment of the whole chromosome complement of the cell among the resulting daughter nuclei. The number of mitotic aberrations occurring during the period of the first division is small as compared to the irregularity occurring in subsequent development.

Second divisions of tapetal nuclei begin during the spireme stage of the microsporocytes and are to be found extending into the metaphase stage of the pollen mother cells. Delayed first divisions, and divisions in diploid cells resulting from previous cytokinesis are also observed during this period. Therefore, one finds first and second divisions occurring side by side. The latter may occur in several ways most of which are aberrant. The chromosomes of two closely appressed nuclei in a binucleate cell may unite after the disappearance of the nuclear membranes in the late prophase and form a single metaphase plate (figs. 15, 16). Subsequent division, if carried to normal completion, will give rise to two nuclei that are tetraploid; if a chromosome connection is retained, a single octoploid nucleus will result (fig. 13). Sometimes the connection between daughter chromosome groups is very marked due to almost complete failure of the separatory process (figs. 24, 28). In some instances two normal metaphase spindles are observed (fig. 25), and subsequent completion of their division gives rise to four diploid nuclei (fig. 29). Such tetranucleate cells are infrequently seen. If two metaphase figures are so oriented in a cell that two of their spindle poles coincide (figs. 18, 26), a pair of diploid nuclei and one tetraploid nucleus will result, provided that each division is complete (figs. 21, 27). If one of the divisions is incomplete (fig. 19) the two resulting

nuclei will be hexaploid and diploid respectively (fig. 20). Should both divisions retain chromosome bridges a single octoploid nucleus would result; this condition was not observed to occur. Occasionally one finds trinucleate cells in which one of the nuclei is very small. Such dwarf nuclei, it seems, are produced by the segregation of a few chromosomes during an otherwise normal anaphase (fig. 14). Tripolar spindles are also found during the second division (fig. 22), and in such cases an octoploid number of chromosomes is distributed among the three telophase groups. At times the orientation of divisional figures is so enigmatic as to make the outcome purely speculative. Such appearances are especially evident during diakinesis (fig. 17), and they serve to emphasize the divisional irregularities that may occur. In one case three metaphase groups were observed in a cell. As a general statement it may be said that the later the occurrence of a division, in the plant studied, the greater is the tendency for irregularity in chromosome distribution.

Just preceding the time of final disintegration the tapetum is composed of cells whose nuclei vary from the diploid to the octoploid condition. There are cells containing single diploid nuclei; others have two. Some may have single tetraploid nuclei; others, a pair. There are cells with a single octoploid nucleus, or a hexaploid and a diploid nucleus. In short, a wide difference in nuclear valency is found; and irregular mitosis plays a large part in creating these conditions. Cells containing diploid nuclei are doubtless present because cytokinesis accompanied nuclear division; such cell division is occasionally observed. Cells having single tetraploid nuclei may result similarly, if cytokinesis is present during the second division, or if a second division fails to materialize subsequent to an incomplete first division. The previously described aberrations in the mitotic process can largely account for the remaining cases of polyploidy, and for the variations in nuclear size and shape.

In the aged tapetum fusions of degenerating nuclei occur, and these are also involved in causing variations in nuclear size and shape. Several observations of fusion occurring between nuclei of adjacent cells show definitely that degenerative fusions of resting nuclei are present (fig. 31). No fusions of resting nuclei are seen previous to this stage of final degeneration. Occasional nuclear fragmentation is also observed in the disintegrating tapetum.

DISCUSSION

In reviewing the literature of amitosis it soon becomes apparent that wherever investigators have claimed the occurrence of amitotic division the cells involved were either highly specialized in character, ephemeral,

pathological, or degenerative. Furthermore, in nearly all verified cases of amitotic division there has been no accompanying cytokinesis. One marked exception is reported in lymphocytes (Wilson, 1925) in which cytokineiss reputedly accompanies amitosis. Even here, however, the dominant mode of division is mitotic, and amitosis appears to be rare. It is noteworthy that such cells are of a highly transitory nature; and therefore observed cases of amitosis may, even here, be occurring in degenerating cells. The problem in lymphocytes seems worthy of further investigation. It appears significant that all verified amitosis has occurred in such highly differentiated tissues, and equally significant that it has not been verified in reproductive or meristematic cells.

In view of the preceding statements it is seen that the question of amitosis seemingly concerns itself wholly with nuclear division in highly specialized cells—cells that have an *extremely* restricted line of development. Consequently it cannot, it appears, be regarded as having genetical significance.

The tapetum is one of those highly specialized, ephemeral tissues with which the amitotic mode of division has often been associated; and it would seem that divisional conditions prevalent there might reasonably serve as an indication of divisional methods prevailing in other highly differentiated, multinucleate cells, especially those having a similar nutritive function.

In the tapetum of *Hosta caerulea* the first amitotic appearances occur during the uninucleate stage when the vesicular structure of the nuclei often simulates nuclear budding, or fusion. But that neither of these occurs is shown by the consistently uninucleate character of the cells at this stage. The next period at which the tapetal nuclei falsely suggest amitosis follows immediately after the first division. Those nuclei in which complete division occurs are closely appressed, and those resulting from incomplete division are, in one way or another, connected by a chromatin bridge. Either appearance might easily be mistaken for amitotic division, especially if viewed in isolated cases; but a study in the developmental sequence of the cells involved reveals the true origin of such appearances. It is suggested that many reports of amitosis in the tapetum have resulted from observations made without a complete study of the tapetal development from its youngest stages to its maturity.

The first nuclear divisions occur in the tapetum before it has assumed its truly hyperchromatic appearance, but by the time second divisions begin the cells have markedly increased in size and the nuclear chromaticity has likewise increased. It seems that the tapetum has by this time really begun its activity of storing food to be released at tetrad formation.

These second divisions are of a remarkably aberrant nature. It appears that accumulation of nutritives within the tapetal cells initiates these divisional irregularities. Precisely what the causative factor may be is questionable, though it is perhaps bound up with changes in the density of the cell contents due to food accumulation. Increase in density within the cells might retard the separatory mechanism of mitosis.

The richly chromatic nature of the normal tapetal nuclei is also apparently bound up with the accumulation of food in the cells. This view is supported when it is recalled that very young tapetal nuclei are lacking in hyperchromaticity, undoubtedly because the cells have not yet begun the accumulative processes which so modify their structure. Farmer and Digby (1910) showed, in certain ferns, that tapetal cells which have lost their secretory function have wholly normal nuclei that are lacking in richness of chromatin.

Chromocenters begin to appear in the nuclei just as soon as the tapetal cells start their rapid enlargement and storage. The appearance of chromocenters, too, is apparently linked with the amassing of food in the tapetal cells. Tischler (1921–1922) cites cases where hyperchromaticity and production of chromocenters result from "feeding" tissues with a peptone solution. Such chromatin richness disappears as soon as "feeding" is arrested.

As previously stated, the second divisions occur after the tapetum has become food laden, and this is believed to be the main factor causing incomplete mitoses. In addition, the presence of more than one nucleus within a cell frequently results in a coinciding of spindle poles, and a consequent fusion of two telophase groups, coming from separate nuclei, to form a polyploid nucleus. Such fusions are dependent upon the orientation of the two divisional figures within a cell. Trinucleate cells that result in this manner show one nucleus approximately double the size of each of the others. The inequality of nuclear size in such cells might easily lead one to infer that they were caused by nuclear budding. When an incomplete mitosis accompanies such a "fusion division" (fig. 19) the resulting nuclear appearance is extremely difficult to interpret from mere observation of the resultant resting nuclei (fig. 20). Similar conditions have, at times, doubtless been labelled "amitosis." After most of the second divisions have occurred in the tapetum one finds few cells containing four diploid nuclei. Absence of such tetranucleate cells clearly indicates that few cells complete the two successive divisions in a normal manner to produce a tetranucleate condition. In this connection, however, it must be remembered that cytokinesis may accompany some of these divisions and thus account for the absence of tetranucleate cells in certain cases.

Late appearances simulating amitosis are found in the aged tapetum and are the aggregate result of irregular mitoses combined with degenerative fusions. The nuclei strongly suggest amitotic budding. Appearances at this stage are such as might easily be misinterpreted by the casual observer, but again developmental study clarifies the conditions prevailing. Disintegrative fragmentation of nuclei is occasionally seen at this time and is the only semblance of amitosis to be observed during tapetal development.

SUMMARY

1. Nuclear divisions in the tapetum of *Hosta caerulea* are typically mitotic.

2. No amitosis was seen, excepting occasional fragmentation accompanying nuclear disintegration in aged tapetal cells.

3. Mitotic divisions are highly irregular. The irregularities appear as: incomplete mitoses giving rise to polyploid nuclei, fusions of two prophases to form a single large metaphase plate, fusions of two telophase groups due to converging spindles from a pair of metaphases, and formation of multipolar spindles.

4. Irregularity of mitotic division increases as the tapetum becomes older and reaches its height during the diakinesis period of the microsporocytes.

5. Increased divisional irregularity appears to be correlated with the increase of nutritive material within the tapetal cells, and is seemingly caused by some physiological disability accompanying this accumulation of foodstuffs.

6. Fusions of chromosome groups during divisional processes are dependent upon the orientation of the mitotic figures within the cell; if spindle poles coincide, fusions result.

7. Few tetranucleate cells are seen, indicating that complete regularity through the two successive nuclear divisions occurring in many tapetal cells is the exception.

8. Mitotic irregularities account for amitotic and fusion appearances, and also for variations in nuclear size within a single cell.

9. Degenerative fusions in the aged tapetum also frequently assume amitotic appearances. Such fusions may occur between the nuclei of adjacent cells.

10. The vesicular structure which tapetal nuclei show during the resting stage of the pollen mother cells often simulates amitosis or fusion.

11. The rich chromatin content of tapetal nuclei is seemingly the result of abundant nourishment.

12. First mitotic divisions in the tapetum occur, in general, from the synizetic to the spireme stages of the pollen mother cells. Second divisions take place from spireme stages through the diakinetic periods of meiosis.

13. Irregularities present in nuclear divisions in the tapetum of the plant studied may possibly obtain in other multinucleate tissues, especially those having a similar physiological function.

The writer wishes to express his sincere appreciation to Dr. M. A. Chrysler for the suggestion of this problem and for stimulating criticism offered during the progress of the work.

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Explanation of plates 19 and 20

Drawings were made with an Abbe camera lucida at table level. A Zeiss 10× ocular, and a Spencer 1.8 mm. oil immersion objective, N. A. 1.3 were used. All drawings are magnified ×700.

Plate 19

Fig. 1. Uninucleate tapetal cell having a single large nucleolus. Microsporocytes in resting stage at this time.

Fig. 2. A normal first division in telophase and a resultant binucleate cell.

Fig. 3. Tetraploid nucleus due to an incomplete first division.

Fig. 4. Cells with nuclei in a state of pyknosis.

Fig. 5. Final stage in pyknosis.

Fig. 6. Binucleate cell with closely appressed nuclei in late prophase.

Fig. 7. An incomplete mitotic division, and a cell containing a resultant tetraploid nucleus.

Fig. 8. A normal binucleate cell.

Fig. 9. Tetraploid nucleus such as would result from a failure of the separatory process in the first division.

Fig. 10. Tetraploid nucleus with an amitotic appearance.

Figs. 11a, 11b. Dumb-bell-shaped, tetraploid nuclei resulting from incomplete division.

Fig. 11c. U-shaped, tetraploid nucleus resulting from incomplete division.

Figs. 12a, 12b. Uninucleate cells during resting stage of microsporocytes. The vesicular condition of the nuclei simulates amitosis or fusion.

Fig. 13. Octoploid nucleus produced by an incomplete second division.

Fig. 14. Trinucleate condition, the small nucleus presumably the result of chromosome isolation during the anaphase of a division.

Figs. 15, 16. A tetraploid nucleus in metaphase, shown in two consecutive sections.

Fig. 17. A highly irregular division with multipolar spindle. This is not a group of three metaphases.

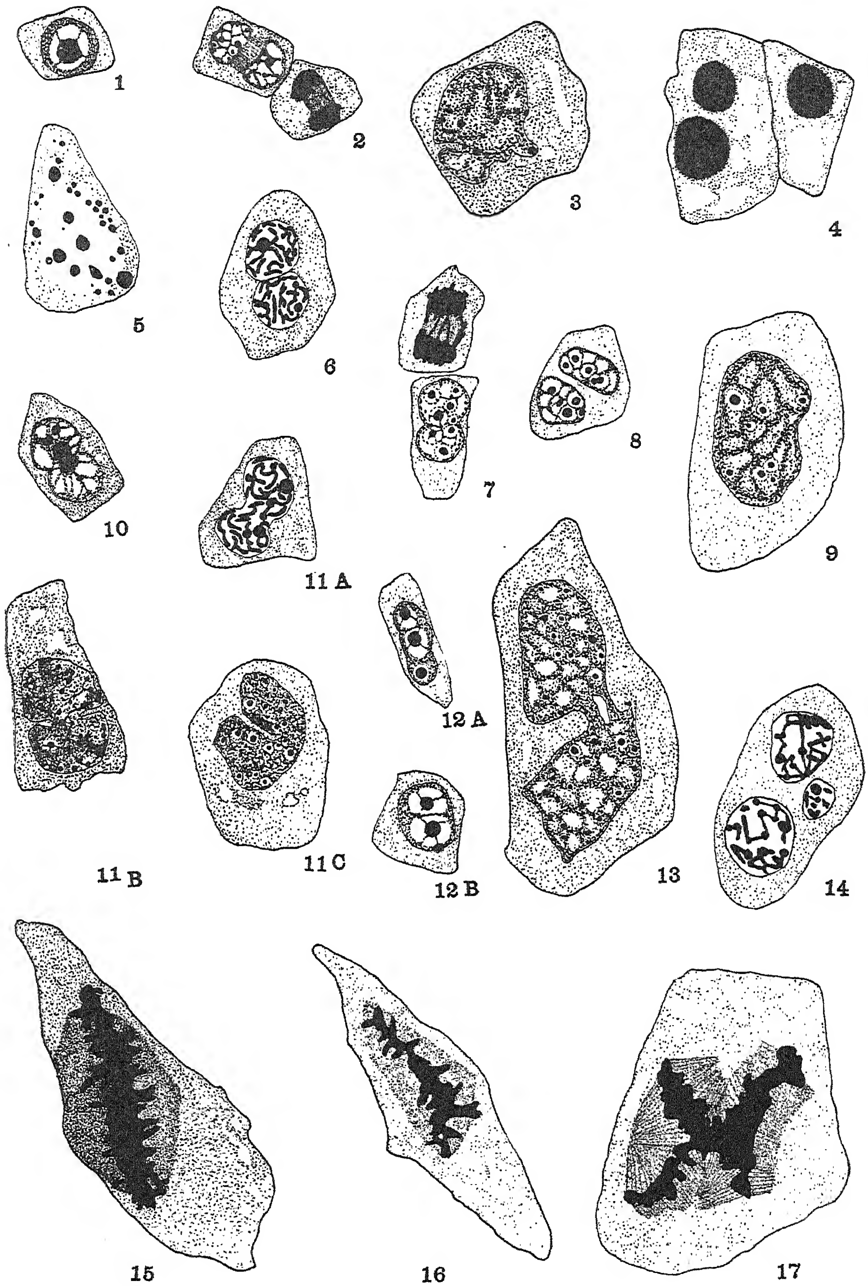

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Plate 20

Fig. 18. A second division showing two telophase groups fusing due to spindle orientation. Two diploid nuclei and one tetraploid nucleus result.

Fig. 19. A second division showing two telophase groups fusing as in figure 18, but one division being incomplete. One hexaploid, and one diploid nucleus are thus formed.

Fig. 20. Cell having a nuclear complement such as would result from the condition shown in figure 19. The nuclei are presumably hexaploid and diploid.

Fig. 21. Trinucleate cell such as would result from the condition figured in 18.

Fig. 22. Tripolar spindle formed by the division of a tetraploid nucleus.

Fig. 23. Tripolar spindle formed during the first division.

Fig. 24. Non-separation during a second division. Note remnant spindle fibers. Resultant nucleus octoploid.

Fig. 25. Two metaphases of a second division. The first division was normal and gave rise to nuclei that were not appressed.

Fig. 26. Fusion of two telophase groups during a second division.

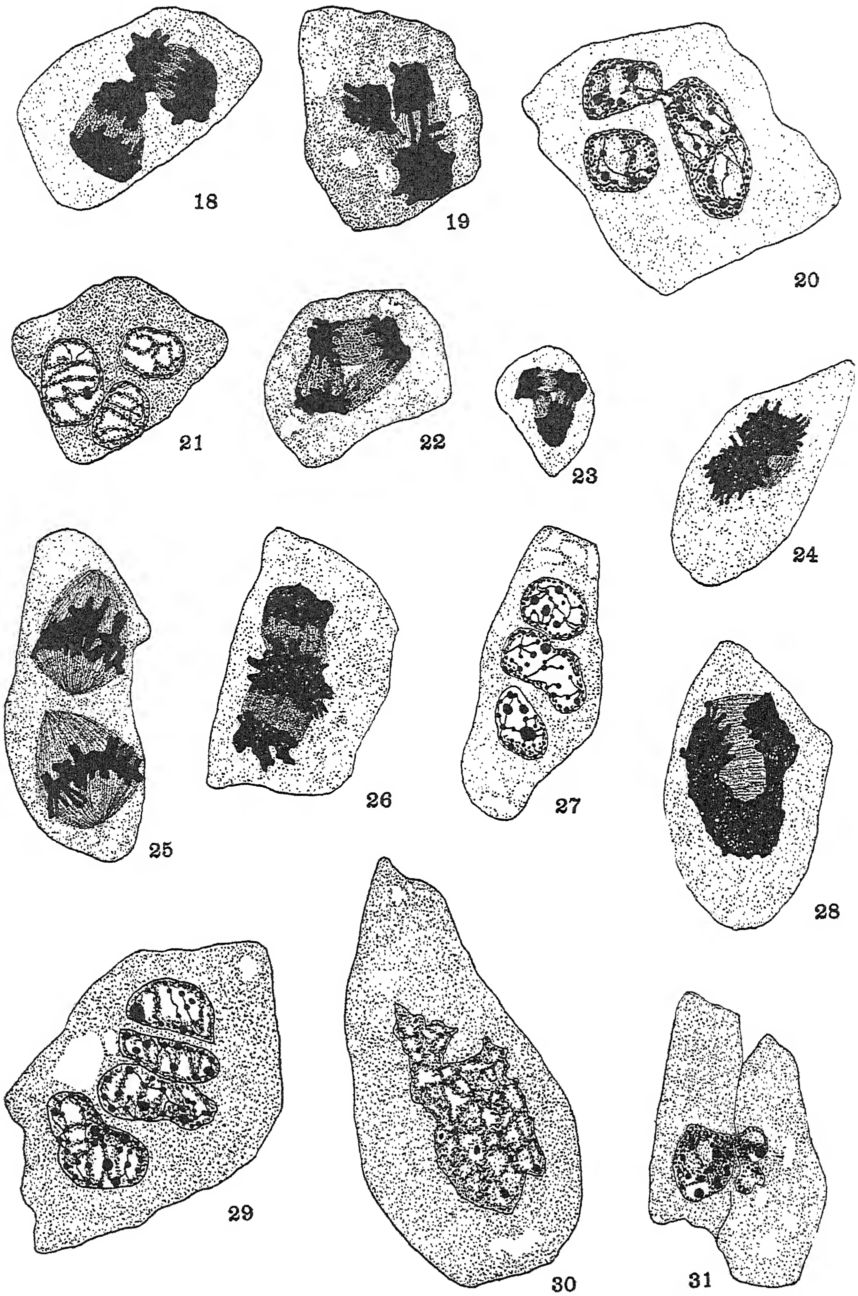
Fig. 27. Trinucleate cell such as might result from the condition in figure 26.

Fig. 28. A second division in which separation was incomplete. A single octoploid nucleus results. Note the spindle fibers.

Fig. 29. Tetranucleate condition resulting from two divisions each of which was complete.

Fig. 30. Cell with octoploid nucleus showing ragged and vacuolate appearance often found in aged tapetal cells.

Fig. 31. Fusion between nuclei of adjacent cells in the aged tapetum.



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1931–1935

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IF ANY of the readers of this journal can furnish any information relative to the identity of the following little-known and poorly described "species," such information will be greatly appreciated by Dr. Harold N. Moldenke, New York Botanical Garden, Bronx Park, New York City, who has for some time been engaged in monographing the American *Verbenaceae*. It is very probable that many of the "species" here enumerated do not belong in the genera in which they have been described, but in each case the original descriptions are so incomplete that their true identity cannot be ascertained readily therefrom. Dr. Moldenke would also appreciate learning where authentic herbarium material of these "species" may be found, since he has thus far not discovered any among the thousands of specimens received by him from 46 of the world's larger herbaria in the preparation of his monographs. It may be that some of these "species" have already been claimed by specialists in other groups who had access to authentic material, and if this is the case, Dr. Moldenke would greatly appreciate this information.

(1) *Aegiphila aurea* Turcz., Bull. Soc. Imp. Nat. Mosc. **36**^{2}: 218. 1863 [based on J. J. Linden no. 131, from Cuba].
(2) *Aegiphila inflexa* Vell. Fl. Flum. **38** (1825), Icon. **1**: 96. 1827 [from Rio de Janeiro, Brazil].
(3) *Aegiphila macrophylla* H.B.K. Nov. Gen. & Sp. Pl. **2**: 251. 1817 [based on Herb. Willdenow 2831, collected by Humboldt & Bonpland in Venezuela].
(4) *Aegiphila punctata* Turcz., Bull. Soc. Imp. Nat. Mosc. **36**^{2}: 219. 1863 [based on a Graham specimen from Jamaica].
(5) *Aegiphila stipulata* Vell. Fl. Flum. **37** (1825), Icon. **1**: 90. 1827 [from Rio de Janeiro, Brazil].
(6) *Aegiphila umbellata* Vell. Fl. Flum. **37** (1825), Icon. **1**: 89. 1827 [from Rio de Janeiro, Brazil].
(7) *Aegiphila virgata* Turcz., Bull. Soc. Imp. Nat. Mosc. **36**^{2}: 220. 1863 [based on a collection of J. Miers from Rio de Janeiro, Brazil].
(8) *Callicarpa reticulata* Sw. Prodr. **31**: 1788 [based on a collection of O. P. Swartz from Jamaica].
(9) *Citharexylum longiflorum* Turcz., Bull. Soc. Imp. Nat. Mosc. **36**^{2}: 208. 1863 [based on R. de la Sagra no. 50, from Cuba].
(10) *Citharexylum lycioides* D. Don, Edinb. N. Phil. Journ., Jan.–Mar. 1831, 238. 1831 [from Mexico].
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(12) *Citharexylum racemosum* Sessé & Moc. Pl. N. Hispan., ed. 1, 103. 1887–90 [from Mexico].
(13) *Citharexylum reticulatum* H.B.K. Nov. Gen. & Sp. Pl. **2**: 257. 1817 [based on a specimen collected by Bonpland at Gonzanama, Peru].
(14) *Scleroon oleinum* Benth. ex Lindl. Bot. Reg. 29, Misc. 65. 1843; *Petitia oleina* (Benth.) Benth. & Hook. f. ex Hemsl. Biol. Cent. Am. Bot. **2**: 539. 1881–82 [based on a cultivated specimen grown from seeds sent by Hartweg from Mexico].

The relation of chromosome pairing to fertilization

G. M. Watkins

During the decades which have elapsed since the modern cytological studies by Strasburger, van Beneden, Boveri, and others on sexuality in plants and animals the concepts as to what constitutes fertilization have changed markedly. Still earlier, as summarized by Johnson (1914), conjugation in *Spirogyra* was observed by Hedwig in 1798 and by Vaucher in 1803, in the Zygomycete, *Syzygites* (*Sporodinia*), by Ehrenberg in 1818, and in several species of desmids (*Closterium*) by Ehrenberg (1838). Unger in 1834 described the spermatozoids of *Sphagnum*, while Thuret (1854) for *Fucus* and Pringsheim (1855) for *Oedogonium* gave perhaps the first accounts of the fusion of heterogametes in the algae. The union of unlike gametes was also discovered in the Oömycetes about this time. Tulasne in 1854 observed the sexual process in *Peronospora*, and de Bary (1863) observed and figured the flow of gonoplasm from the antheridium to the egg in *Pythium*, and also figured a similar process for *Cystopus*. This was perhaps the first and is probably still the most convincing account of a genuine mixing of plasms in a case in which the sex differences characterizing maleness and femaleness are well marked. Fertilization by mixing through a fertilization-tube was seen in *Saprolegnia* and *Achlya* by Pringsheim (1858). Spermatozoa were seen within the ova of the rabbit by Barry (1843).

In spite of de Bary's development of the gonoplasm concept, the majority of early workers came to regard fertilization, especially in algae and fungi, and on the basis of the *Spirogyra* data, as the "fusion of two apparently homologous cells." This view involved primarily the union of protoplasts, without particular regard to the activities or fate of the various cell constituents.

This concept of fertilization dominated biological thought until the studies of Hertwig (1877 a and b), Strasburger (1877), and Schmitz (1879) revealed that in both plants and animals the union of the gametic protoplasts may be followed directly by the fusion of gametic nuclei. The most advanced view, perhaps, of that time was expressed by Strasburger (1877, p. 509) in the following generalization:

"O. Hertwig ist der Ansicht, dass die Befruchtung allgemein auf der Copulation zweier Kerne, des Kerns des Spermatozoiden und des Eikerns, beruht, in dieser Ansicht stimme ich mit ihm überein, erweitere sie aber darin, *dass*

[The Bulletin for June (62: 301–368) was issued June 1, 1935]

eine Copulation auch zwischen den übrigen gleichwerthigen Bestandtheilen des Spermatozoiden und des Eies vor sich geht."[1]
In this contribution Strasburger definitely committed himself to the view that fertilization consists of more than a gross plasmatic fusion. It involves also a union of equivalent parts of the gametes. Schmitz (1879) upheld this view by showing in stained preparations that gametic nuclei of *Spirogyra* move together and fuse after the protoplasts have united. That the behavior of the nuclei in the zygospore of *Spirogyra* is as simple as Schmitz reported was later brought into doubt by the work of Chmielevsky (1890).

Further evidence that protoplasmic fusion (plasmogamy) is followed immediately by the union of gametic nuclei (karyogamy) appeared in the expansive and careful studies by van Beneden (1883), Boveri (1890), and many other workers. This came to be regarded as the essential characteristic of fertilization, and subsequent data have shown that syngamy of this type occurs in the majority of plants and animals. During this period, however, Klebahn (1888) showed that in many Conjugatae plasmogamy occurs without being immediately followed by karyogamy. A thick-walled binucleate zygote is produced, which may endure thus, as he reports, for many months, finally undergoing karyogamy at the time of germination. Raciborski (1896), in studying zygote formation in *Basidiobolus ranarum*, by controlling the cultural conditions was able to delay karyogamy for varying lengths of time. In some cases the binucleate zygote was caused to germinate, producing, as reported, a binucleate germ-tube. Raciborski concludes that two definite phases are to be distinguished in fertilization, namely, fusion of protoplasts as wholes and fusion of gametic nuclei. In case plasmogamy is separated from karyogamy by a dikaryophase of several or many cell generations, the cell in which the nuclei at last fuse was termed by Raciborski the *zeugite*. In animals a similarly delayed karyogamy was described for *Cyclops* by Rückert (1895) and Häcker (1895), who showed that the individuality of the parental nuclei is maintained through several successive gonomeric divisions in the early development of the embryo. Later B. G. Smith (1919) demonstrated a similar condition in *Cryptobranchus* extending in all nuclei of the embryo through the fourth cleavage mitoses.

Poirault and Raciborski (1895) and Sapin-Trouffy (1896) found that karyogamy takes place in the Uredinales in the mature teleutospore, thus ending the long dikaryophase which had been known (Schmitz, 1880) to exist throughout most of the rust life cycle. It was later shown by Blackman (1904), Christman (1905, 1907), and Blackman and Fraser (1906)

[1] My italics.

that the dikaryophase in several species is initiated by nuclear migrations or cellular fusions in certain sub-aecidial hyphae. Thus far the data on sexuality in fungi and algae left unsettled the question of the function of the spermatia in the rusts. According to Meyen's (1841) early suggestion, the products of the spermogonia and aecidia are to be regarded as male and female gametes respectively, and Blackman's figures of nuclear migrations tend to uphold this, indicating, however, that the spermatia are vestigial male gametes and that certain vegetative hyphae near the "female" hyphae in the base of the aecidium have become transformed into functional male gametangia. The studies of Craigie (1927 a and b, 1928, 1931), pointing out the heterothallic nature of some rusts, and that the union of the products of plus and minus strains of sporidia is necessary for the production of aecidia, marked the beginning of a new epoch in the study of sexuality in fungi. Miss R. F. Allen (1930, 1932, 1933) and Andrus (1931) report that the binucleate condition may arise perhaps by the fusion of spermatia with certain receptive hyphae which protrude through the stomata of the host. Andrus has compared these receptive hyphae with the trichogynes of the red algae and many ascomycetous forms. As suggested by Miss Allen (1933, p. 11), the recent discovery of fertilization through the union of spermatia with receptive hyphae seems incompatible with the older accounts of Blackman and Christman. Considered from the present-day standpoint it seems that different species of rusts may differ in the manner of origin of the binucleate condition, yet it is nonetheless characteristic of the majority of species so far investigated that the entire sporophytic phase is composed of binucleate cells, karyogamy in the mature teleutospore being followed immediately by meiosis and a return to the haploid condition.

The rise of interest in heredity during the last thirty-five years has directed much attention to nuclear phenomena, and especially to the chromosomes, since evidence points to them as the possible conveyors of hereditary and morphogenetic factors. In this connection one of the most important characteristics of the nuclear constituents is the so-called paired condition of the diploid chromosomes, which supposedly is the attainment of the definitive relations between the parental chromatin elements. If indeed the chromosomes are the primary carriers of hereditary factors, it is in this relation only, according to current views, that these factors can be blended, balanced, and distributed to the posterity of the organism. Thus fertilization has come to be considered as essentially the conjugation of homologous chromosomes, which, in the possibilities thus achieved, provides for crossing over, translocation, segmental interchange, etc. In the above quotation from Strasburger may be seen an early forecast of this

idea, and another interesting view was expressed by Johnson (1914):

"The essence of the sexual process then, as far as yet morphologically demonstrated, consists not of a real fusion, but merely of a temporary association, followed by a reassortment at sporogenesis, of those ultimate, inheritance-bearing units—the chromosomes."

In the majority of plants and animals studied the chromosomes are so far figured and described as paired only in meiosis, at the end of the diploid phase of the life cycle. But evidence by Strasburger (1905), Müller (1909, 1912), Metz (1914, 1916), and many others shows that in certain species of plants and animals the chromosomes are paired during divisions of diploid somatic nuclei. Among plants *Yucca aloifolia*, *Y. draconis*, *Y. guatemalensis*, *Galtonia candicans*, *Pisum sativum*, *Oryza sativa*, and others, and among animals a large number of species of the Diptera exhibit paired chromosomes in somatic mitoses. This pairing, as figured in the literature, is usually not as close as that found later at synapsis, as can readily be determined by comparing the mitotic figures given for such forms by Strasburger (1905, 1907), Müller (1909, 1912), and Metz (1914, 1916) with, for example, those of C. E. Allen (1905) for the synaptic and post-synaptic stages of *Lilium canadense*. It, however, indicates an expression of the same tendency, the earliest possible expression of which is the pairing of the chromosomes immediately during and after karyogamy.

Recent reports by Heitz and Bauer (1933) and Painter (1934) indicate that such complete chromosome conjugation may not necessarily be confined to the meiotic prophases. In follicular cells of the ovary, cells of the malpighian vessels, salivary glands, and intestinal walls of *Bibio hortulanus*, Heitz and Bauer describe prophase figures in which bivalent chromosomes corresponding to the haploid number are seen. According to their figures the members of each pair can be seen to conjugate point for point throughout the entire length of the homologues, until complete synapsis is accomplished. These figures (Heitz and Bauer, 1933, figs. 1a and 2a-c) are strikingly similar to the late prophases of meiosis, particularly diakinesis, with the homologous chromosomes closely paired and showing numerous chiasma-like unions. As figured by them the prophases of mitosis in these cells are essentially like typical meiotic prophases, with the exception that the synizesis or contraction stages are lacking. Painter's account of the conditions in the salivary glands of *Drosophila melanogaster* agrees essentially with the report of Heitz and Bauer, with the additional observation of the failure of pairing in certain segments of the bivalents where inversions were said to have occurred. It is highly interesting and significant to

note this departure from the older concepts of synapsis as an event peculiar to meiosis. According to the current views of crossing over, segmental interchange, etc, and the genetical data based on them, the homologous chromosomes have been regarded as bodies remaining discrete and immiscible throughout the thousands of successive somatic mitoses following fertilization, but changing character more or less completely during the brief period of meiosis involving intimate conjugation, sticking together, and interchange of parts. These views, postulating a high degree of particulate specificity in the relation of the conjugating chromosomes, are hardly compatible with the present-day conceptions of the colloidal nature of protoplasm. If the union of homologous chromosomes in somatic cells is as intimate as that described by Heitz and Bauer and by Painter, there is no *a priori* reason why chiasmatypy should not characterize somatic as well as meiotic synapsis. In general the widespread occurrence of non-meiotic synapsis and crossing over, especially in cells destined to give rise ultimately to the reproductive cells, would provide the mechanism for almost any assumed heterogeneous or alternative types of inheritance as well as the mendelian, and would perhaps afford a better basis for the assumption that the chromosomes are the material of heredity. However, the manifestation of mendelian inheritance by an organism in which somatic synapsis is a general occurrence might be taken as implying that the characters of the progeny are determined by some extrachromosomal agency. The implication is very strong that the promiscuous occurrence of synapsis in somatic nuclei, with the attendant manifold possibilities of chiasmatypy, is incompatible with the assumption of the genetic individuality of chromosomes with the genes in a linear series.

Miss Fraser (1912) has pointed out the wide variations in the behavior of parental chromatin elements following syngamy in different organisms, emphasizing especially the marked differences between such forms as *Galtonia candicans*, in which the chromosomes are paired in somatic divisions, and the rusts, in which karyogamy does not occur until almost the end of the diploid phase. Abundant data in this connection have been accumulated since the publication of her paper, and it is the purpose of the present discussion to align these more recent facts with the older in a schematic series based upon her suggestions. The life cycles of species representing the salient positions in the series are illustrated in the accompanying diagrams and include the facts gained from my recent study of chromosome arrangement in somatic nuclei of *Yucca rupicola* Scheele. (See text fig. 1.)

As Clemens Müller (1909) showed for *Yucca aloifolia*, *Y. draconis*, and *Y. guatemalensis*, the nuclei in root tips of *Y. rupicola* also contain a com-

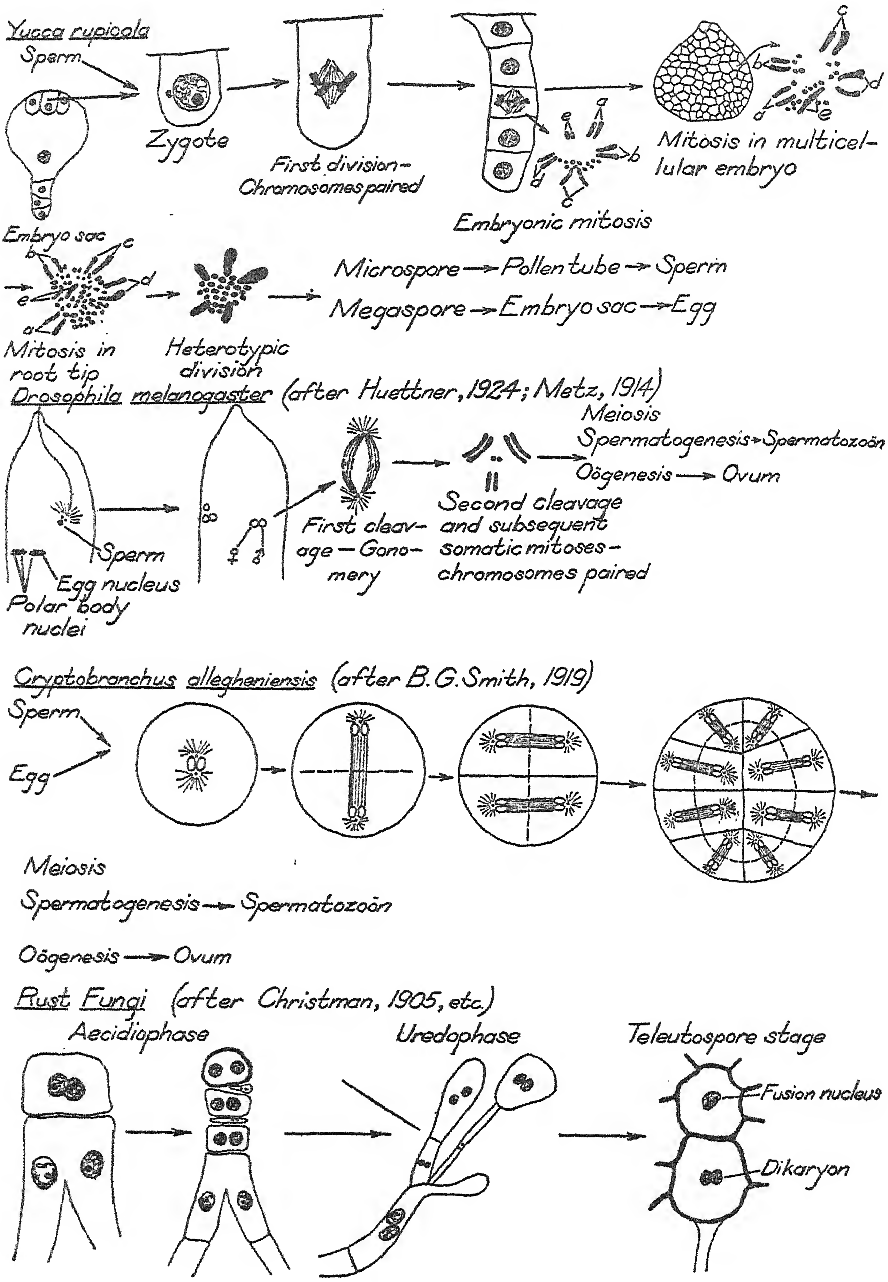

Fig. 1. The life cycles of several organisms, illustrating the variations in the behavior of gametic chromatin after syngamy.

bination of both long and short chromosomes (the diploid number in *Y. rupicola* is sixty, of which ten are large and fifty small), which are arranged in pairs upon the equatorial plates of all somatic mitoses studied —in root tips, in ovarian cells, and in cells of young embryos, including the equatorial plate of the first division of the zygote. These data indicate that the homologous chromosomes become associated in pairs during or immediately after karyogamy, appear thus upon the equatorial plate of the first embryonic division spindle, and continue to occur in this paired relation in each equatorial plate stage throughout the entire diploid phase. A study of the meiotic prophases of *Y. rupicola* seems to indicate that the culmination of this condition is a typical chromosome conjugation in synapsis similar to that described for *Lilium* (C. E. Allen, 1905).

For *Yucca* the three phases of fertilization which have been recognized above—plasmogamy, karyogamy, and pairing of homologous chromosomes—appear as essentially a single process. So far as I find from the literature it is the only organism in which cell fusion is followed so promptly by chromosome pairing. It stands as one extreme in such a series as is above set forth.

Huettner (1924) reports for *Drosophila melanogaster* that, following the coming together of the gametic pronuclei in the resting condition, the chromosomes appear in two gonomeric groups side by side on separate spindles at the first cleavage division. On the second division spindles the evidences of gonomeric separation have completely disappeared, and the homologous chromosomes are closely paired. Huettner (1923) and Metz (1914, 1916) had previously shown that this paired condition persists throughout the remainder of the diploid development of *Drosophila.* The gonomeric independence of the parental germ plasms in the first cleavage gives way to the perfect chromosome pairing of the second division. Such sharp transitions are not provided for in current theories of nuclear and chromosomal activities.

The persistence of the paired arrangement throughout almost the entire diploid phase, as well as the almost diagrammatic perfection of the pairing found in a large number of dipteran species, as reported and figured by Metz, are sufficient grounds for assuming that *Drosophila* and other similar forms occupy the next position in a series based on the time at which chromosome pairing appears.

Next perhaps, for the present, may be placed the great majority of plant and animal species, since in most forms plasmogamy and karyogamy are both accomplished as the ordinary type of syngamy, but chromosome pairing, as reported at least, does not occur before synapsis in the meiotic prophases. Several factors should be considered in connection with the

massing of all these forms into a single group. In the first place the number of authors who have considered chromosomes from the standpoint of pairing in somatic divisions is relatively small, and many cases in which the tendency to pair is exhibited have probably been overlooked or ignored by investigators who were primarily concerned with other problems. Also it is a noteworthy fact that the majority of species in which pairing in somatic nuclei has been observed are characterized by relatively long, rod-shaped chromosomes. In *Yucca*, with its complement of a mixture of long and very short chromosomes, Müller (1909) noted that the pairing is more evident in the rod-shaped than in the very short chromosomes, and my results with *Y. rupicola* confirm this. The large chromosomes in the nuclei of *Yucca* are much less numerous than the small ones; doubtless the visible evidence of pairing in somatic nuclei is inversely proportional to chromosome number. The literature on these various points is to a certain extent conflicting. Thus, while such long chromosome forms as *Galtonia candicans*, *Pisum sativum*, *Eucomis bicolor*, *Hyacinthus orientalis*, *Chionodoxa lucillae*, and many others have been described (Strasburger, 1905, 1907; Müller, 1909, 1912) as showing pairing in the somatic mitoses, in many other forms, also having relatively long chromosomes, such as species of *Allium*, *Lilium*, *Trillium*, *Vicia*, *Podophyllum*, *Crepis*, etc., the chromosomes have been frequently figured and described by various authors with no reference to a possible paired arrangement during these stages. Furthermore, for the somatic nuclei of *Spinacia oleracea* (Stomps, 1910) and *Mouriria anomala* (Ruys, 1924), in which the chromosomes are figured as quite short, close pairing has been described. The relation between chromosome number and recognizable pairing is certainly not rigid, since there are many species with few chromosomes, such as *Crepis capillaris* ($2n=6$), in which the diploid sets are usually figured with little evidence of pairing. In *Beschorneria superba* ($2n=$ ca. 50), on the other hand, Müller (1912) recognized marked chromosome pairing.

In a few species of plants and animals the individuality of the parental chromatin complexes is maintained for a brief period after plasmogamy has taken place. Gonomery is reported for the first division of the embryo of *Pinus* by Miss Ferguson (1904). In species of *Cyclops* Rückert (1895) and Häcker (1895) have demonstrated the persistence of parental chromatin groups in the form of double nuclei which occur in all cells up to the eight-celled stage. According to Rückert for *C. strenuus*, all the cells of the thirty-two-celled embryo are binucleate. In later embryonic stages some of the cells are uninucleate as a result of karyogamy, but a few binucleate cells can be observed as late in the larval development as the time of formation of the three pairs of nauplius extremities. For *Crypto-*

branchus B. G. Smith (1919) has reported a condition of gonomery which persists through four successive cleavage divisions in the development of the embryo. Evidences of the individuality of the parental nuclear elements were seen in some nuclei in the gastrula stages. These forms stand intermediate in the series, since in them the process of plasmogamy initiates the diploid phase, karyogamy occurs sometime later in embryonic development, and so far as is reported, pairing of the chromosomes becomes recognizable only in the prophases of the reduction divisions. All three so-called phases of fertilization are well separated.

Various species of fungi represent the other extreme of such a series. Within this group the nuclear conditions are very diverse and frequently as yet imperfectly understood, but the nuclear phenomena in the Uredinales furnish an example of the greatest possible separation between plasmogamy and karyogamy. As mentioned above, the diploid phase is initiated by nuclear migrations or cellular fusions among the subaecidial hyphae (Blackman, 1904; Christman, 1905), or by fusions of spermatia with receptive hyphae somewhat prior to the formation of the aecidia (R. F. Allen, 1930, 1932, 1933; Andrus, 1931). Nuclear fusion does not follow immediately, however, and the rust goes through a long and profuse dikaryonic development. The uredospores are binucleate and the dikaryophase ends only with the maturing of the teleutospores. These are the so-called zeugites, and in them karyogamy occurs (Poirault and Raciborski, 1895; Sapin-Trouffy, 1896), only to be followed immediately by meiosis, which brings about the haploid condition in connection with the production of the promycelium and the sporidia.

From the cases of gonomery reported by Rückert, Häcker, B. G. Smith, and others it is seen that the union of parental nuclei may be a very gradual process, that they do not approach each other and, as two drops of water, suddenly plunge together because of surface tension forces. The approach and fusion of nuclei in *Cyclops*, for example, extends through several mitotic generations, the association gradually becoming more intimate until at last the dual structure of the nuclear mass in each cell is detectable only in interkinesis by the presence of a very slight median constriction or a very faint partitioning membrane between the homologous halves. In the well-known case of the rusts the union of parental nuclei is not at all necessary for the development of the sporophyte. Through countless mitotic generations the nuclei persist as separate entities. In the light of the recent evidence presented by Heitz and Bauer and Painter for the widespread possibility of synapsis in diploid somatic nuclei the extreme nuclear conditions exhibited by *Yucca* and some of the Diptera on the one hand, and by many of the Uredinales on the other,

as well as all the known intermediate conditions, must certainly be taken into account as a possible vehicle for many varying types of hereditary phenomena.

My sincere thanks are due to Professor R. A. Harper and Professor J. S. Karling for many valuable suggestions given me during this study.

SUMMARY

1. The composite results of many investigations on the nature of the sexual process in plants and animals indicate that in general three definite phases are to be distinguished, namely, fusion of protoplasts as wholes (plasmogamy), fusion of gametic nuclei (karyogamy), and pairing of the homologous chromosomes.

2. From the standpoint of its effect on inheritance the last-named phase, the pairing of homologous chromosomes, has been greatly emphasized.

3. Different organisms vary strikingly in the interrelationships of the three phases of fertilization. *Yucca* shows chromosome pairing immediately after karyogamy, at the beginning of the diploid phase, and species of the Uredinales undergo karyogamy only at the end of the sporophytic development. These are extreme conditions and such forms as *Drosophila*, *Lilium*, *Pinus*, and *Cyclops* stand intermediate in the series.

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Notes on Texas phloxes

Eula Whitehouse

A study of several hundred specimens from the large eastern herbaria and many more from Texas field and herbaria sources has brought to light a number of interesting facts in relation to the annual phloxes. Those who have studied the annual phloxes in their native habitat have long felt the need of a study which would bring into harmony descriptions and field specimens.

Five annual species of *Phlox* have been described as natives of Texas. The first of these was *Phlox Drummondii*, described by Hooker (1835) from seed sent by Thomas Drummond. Gray (1870) recognized two varieties of *Phlox Drummondii, villosissima* and *tenuis*, but later (1886) notes that *tenuis* is "seemingly very distinct." This classification was maintained by Coulter (1892), but subsequently Nelson (1899) gave specific rank to *tenuis* and Small (1903) to *villosissima*. Brand (1907), in his monograph of the genus *Phlox*, adds to the confusion by reducing *P. tenuis* and *P. villosissima* to varieties of the subspecies, *eu-drummondii*, of *Phlox Drummondii* and adding a new subspecies, *glabriflora*. *Phlox roemeriana* was described by Scheele (1848) from specimens carried back to Germany by Roemer. Nelson (1899) added *P. aspera* to the list of annuals, but suggested that it might possibly prove to be a perennial. Brand recognized *Phlox roemeriana*, but considered *P. aspera* as a variety of *P. Drummondii.*

Of these five species, *P. Drummondii, P. tenuis*, and *P. roemeriana* are undoubtedly distinct species and will be discussed in a later article. *Phlox aspera* Nels. is considered by Wherry (1930) to be a perennial, which he classes as a variety of *P. pilosa* L. The status of *P. pilosa* as exemplified by Texas specimens needs further study, for a great range of variability is shown by specimens assigned to this species. The present study has shown that *P. villosissima* (Gray) Small should be placed in the perennial group, closely related to *Phlox pilosa* L.

Phlox villosissima (Gray) Small is based upon Wright's specimen 1656 from the "pebbly bars of the Nueces River, S. Texas." The type at Gray Herbarium, as well as cotypes at Gray and Field Herbaria, clearly shows perennial characteristics. The label on the type bears the inscription, "*Phlox Drummondii,* Hook. var. *viscosissima,* Gray." The thick, glutinous leaves make "viscosissima" as appropriate a name as "villosissima." Only a few specimens have been found showing the characteristics of Wright's type specimen. Further study may reduce it to an ecological form, for it grows in an unusual environment for a phlox.

The confusion which has arisen in the determination of phloxes from

Southern Texas has resulted from this description of *P. villosissima* as an annual, an error easily accounted for by the absence of lower leaves from the type and the close resemblance of its long woody tap-root to an annual root. Another cause is the distribution of Heller's specimen 1435, collected on Nueces Bay in 1894 and incorrectly determined and distributed as *P. Drummondii villosissima* Gray. This classification was followed by Brand (1907), but Nelson (1899) thus assigns it doubtfully.

As Wright's specimen stated that it was found on pebbly bars, the writer, in trying to re-locate the type locality followed the suggestion of Dr. B. C. Tharp to look in the vicinity of Uvalde, where the Nueces River cuts through the southwestern edge of the Edward's Plateau and where bars of chalky gravel are numerous in the wide bed of the river. Numerous plants which closely matched the type were found at two crossings of the Nueces near Uvalde. A fruitless search was made on the lower course of the river, where the channel narrows and deepens and there are no gravel bars.

The unusual habitat of this phlox is worthy of special note. The gravel in which the scattered plants are found is unusually coarse and sometimes quite deep, so that the long woody perennial roots on some plants extend three or more feet. The plants are afforded some shade in morning or evening from scattered trees or shrubs several feet away.

The pubescence of different plants collected at the two crossings varied considerably, being very dense on some and scant on others. Plants on the Medina River growing on a shady bank in rich humus are even less pubescent and viscid and grow much taller.

Specimens examined which check carefully with the type are as follows:

Texas: Without definite locality—Wright 1656 (G, F), Lindheimer 467 (ANS), Bigelow (F), Pope (G); Sutton County—Sonora, Jones 1013801 (M); Pecos County—Sheffield, Jones 28281 (M); Val Verde County—on Devil's River, Orcutt 6059 (M); Real County—Leaky Tharp (T); Uvalde County—Laguna to Brackettsville on W. Nueces R., Whitehouse (T), sw. of Uvalde, Whitehouse (T). A densely villous specimen of *Phlox pilosa* L. from Granite, Greer County, Oklahoma, needs further study. With the exception of this and Bigelow's specimen, the range of *Phlox villosissima* seems to be confined to the streams of the limestone hills of Central and Southwestern Texas.

In the vicinity of Nueces Bay, the phlox distributed by Heller grows very abundantly in sandy wooded regions. Its relationships need further study, being intermediate between *Phlox Drummondii* Hook. and the plant so abundant on the sandy prairies south of the Nueces River, which Brand has called subspecies *glabriflora* of *Phlox Drummondii*.

Careful field and herbarium study has convinced the writer that this southern annual *Phlox* is worthy of specific rank. It grows abundantly on sandy prairies south to Raymondville, Willacy County and westward to the southern parts of Duval and Webb Counties. Except on boundary lines, these plants show little variation and agree quite closely with Brand's characters of a branched habit, glabrous corolla tube and lanceolate leaves.

Brand cites as specimens of this subspecies *glabriflora* Wright 1656 and Berlandier 2526 (Herb. DC), not giving the herbarium in which the Wright specimen belongs. This admits of some confusion, as Wright 1656 (Gray Herbarium) is the type of *Phlox villosissima*. Another specimen collected by Wright and distributed as 1656 is *Phlox roemeriana* Scheele. The fact that Wright's route across Southwestern Texas lay about a hundred miles northwest of the present known western limit of *Phlox glabriflora* suggests that the specimen which Brand cites may have been erroneously attributed to Wright. However, a few specimens collected by Small and Wherry 11803 (NY) near Orange, Apr. 11, 1925, are much further out of range. Brand undoubtedly errs in giving New Mexico as the type locality of Wright's specimen, for no annual phloxes are found west of the Pecos River. Judging from other specimens collected by Wright, the number would indicate that it came from the region between San Antonio and Del Rio.

A number of specimens of Berlandier's collection 2526 represented in our eastern herbaria have been examined. Berlandier's notes indicate that he was familiar with the plant throughout the region where it is most abundant. The specimen at Philadelphia bears the notation, "fl. violacei. in locis arenosis. De Matamoras a las Nueces April, 1834." At Gray Herbarium and Missouri Botanical Garden the label is the same except for the locality which reads, "Del Arroyo Colorado al Rio de las Nueces." These and other specimens without data (ANS, F) all show the characteristics noted by Brand.

Few variations have been observed in *Phlox glabriflora*. The flowers do not have the "phlox-purple" color of some of the other annuals, but are paler, the color varying from pink to lavender and fading blue. White flowers have been noted at Redfish Bay by Dr. Tharp. The flowers when pressed usually show a bluish color along the margins of the lobes. The plants from Redfish Bay likewise vary in having a very short style and some have almost eglandular pubescence. In older plants showing long continued branching, the leaves have a tendency to become broader and shorter, but still remain lanceolate in shape.

Phlox glabriflora is markedly different from the other annual species of *Phlox* which have been described, but is more closely allied to *Phlox*

Drummondii Hook. than to *Phlox tenuis* (Gray) Nelson or *Phlox roemeriana* Scheele. It varies from the former in its short, glabrous corolla tube, its thin, narrow, lanceolate, non-viscid leaves, its flattened calyx lobe tipped with a short callous point, and its widely branched habit.

Phlox glabriflora (Brand) Whitehouse, n. comb.

Phlox Drummondii Hook. subspecies *glabriflora* Brand in Engler's Das Pflanzenreich IV. 250: 71. 1907.

ROOT: annual, a long primary from which, in widely branched plants, arise two large branches 3–5 cm. below the soil surface. STEM: central 15–30 cm. long, erect, pubescent above with long, soft, mostly eglandular hairs and almost glabrous below, the mid-portion larger than the slender base; basal branches numerous, opposite, glabrous and slender below, decumbent-ascending; upper branches 2–3 alternate, slightly pubescent; basal internodes very short, 1–5 mm., the upper increasingly longer, 1–2 cm. LEAVES: lower linear-lanceolate with narrowed bases, longest at the third and fourth nodes, $6\frac{1}{2}$ cm. long and $2\frac{1}{2}$ mm. wide, thin and almost glabrous; upper lanceolate-acuminate, base narrowed to rounded, but scarcely clasping, alternate, pubescent with a few soft scattered hairs; bracts lanceolate-acuminate, 10–15 mm. long; branch leaves linear-lanceolate, often ensiform, 2–4 cm. long. INFLORESCENCE: loosely cymose, the peduncles commonly 4–5-flowered, 2–4 cm. long, stout; terminal flower pedicel 5 mm. long or less, the axillary pedicels much longer, stout. CALYX: 9–10 mm. long, the lobes slightly longer than the tube, pubescent with numerous long, slender hairs, eglandular or tipped by small glands, mid-nerve conspicuous even in flower, extending visibly about $\frac{3}{4}$ length of the calyx and giving a keeled effect to the calyx tube, the two lateral nerves being visible only about $\frac{1}{2}$ the length; lobes linear, flattened, slightly thickened with a short acute callous tip, spreading or recurved in flower, but erect in fruit. COROLLA: tube pale pink, glabrous, with a broad base showing a sharp constriction 2 mm. up, 10–15 mm. long but commonly 13 mm., the upper stamen attached near the apex of the tube, inner basal hairs inconspicuous; lobes obovate to cuneate, apex acute or rounded, 9 mm. long and 8 mm. wide, lavender, sometimes pink, white or blue, mid-vein darker and two conspicuous oblong white spots near the base; throat white, slightly funnel-shaped, 2–3 mm. broad. PISTIL: about $3\frac{1}{2}$ mm. long, enclosed in the minute, greenish disc; stigmas linear, $1\frac{1}{4}$ mm. long; style narrow, $\frac{1}{2}$–1 mm. long; ovary ovoid, $1\frac{1}{4}$ mm. long, carpels 1-ovuled. CAPSULE: ovoid, 5–6 mm. high. SEED: 3, light gray, elliptical-oval, $3\times1\frac{1}{2}$ mm., not winged, shallowly rugose.

Phlox glabriflora (Brand) Whitehouse. n. comb.
(*Phlox Drummondii* subspecies *glabriflora* Brand.)

Caulis herbaceus, ramosus, superior hirsutis longis mollissimis pubescens et inferior glabrus. Folia infima petiolata linearia-lanceolata, opposita, glabra, $6\frac{1}{2}$ cm.$\times2\frac{1}{2}$ mm.; media alternata, sessilia lanceolata-linearia; summa e basi

latiori lanceolata. Rami oppositi e basi, multi. Pedunculi 2–4 cm. longus, validi. Calyx 9–10 mm. altus, hirsutus, laciniae lineares tubo paulum longiores, abrupte apiculatus. Corolla lilacina, tubus 13 mm. longus, glabrus, limbi laciniae obovatae vel cuneatae, 9–10 mm. longus, albae circum oculum. Ovarium ovatum, loculis 1-ovulatis. Capsula 5–6 mm. alta.

Distribution: Nueces County to Willacy and Webb Counties, abundant; Orange County, rare; from the Nueces River to the Medina River, rare.

Specimens examined:

Brooks County—near Falfurrias, April 6, 1931, McKelvey 1745 (US); March 6, 1934 and July 16, 1925, Tharp (US, T); July 17, 1930, Wolff 2419 (US); March 17, 1934, Whitehouse (T); Cameron County—May 10, 1900, Bailey 247 (US); March 20, 1908, York (US, T); Jim Hogg County—Hebbronville, Feb. 13, 1919, Hanson 343 (G, US, T); March 15, 1931 and March 5, 1934, Tharp (US, T); March 17, 1934, Whitehouse (T); Kennedy County—Sarita, Apr. 11, 1905, Lewton 124 (ANS, US); Feb. 1829, Berlandier 532 (ANS); Kleberg County—Riviera, Feb. 23, 1931, Harrison (US); March 15, 1931, Tharp (T); March 17, 1934, Whitehouse (T); Nueces County—Mustang Island, April 16, 1933, Whitehouse (T); Orange County, April 11, 1925, Small and Wherry 11803 (NY); Webb County, March 5, 1934, Tharp (T); Willacy County—Redfish Bay, March 5, 1934, Tharp (T); between Nueces and Medina Rivers, Jan. 1853, Thurber (G); without definite locality, Apr. 1834, Berlandier 2526 (ANS, F, G, M).

The preceding list includes only the forms with a glabrous corolla tube. Along the boundaries, various forms with pubescent corolla tubes show evidence of hybridization and these will not be reported without further investigation. The specimens listed from Cameron County were probably collected in the northern part which has since been cut off into Willacy County.

Grateful acknowledgment is made to Dr. B. C. Tharp for his plant collections, assistance in borrowing material, and especially for his field work in 1931 and 1934 in checking the distribution of the annual phloxes. Appreciation is also extended to the curators of the various herbaria who have assisted with the loan of material. The following list includes the herbaria from which specimens were borrowed and the abbreviations used in referring to them:

ANS—The Academy of Natural Sciences of Philadelphia.
B—Brooklyn Botanical Garden.
F—Field Museum of Natural History.

G—Gray Herbarium of Harvard University.
M—Missouri Botanical Garden.
NY—New York Botanical Garden.
NT—North Texas State Teacher's College.
US—United States National Herbarium.
T—University of Texas Herbarium.

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Observations and experiments on sex in plants[1]

John H. Schaffner

Because of the complexity and diversity of sexual phenomena in the plant kingdom, many points having a bearing on the theory of sex are still obscure and many who deal with the subject are apparently unacquainted with this complexity and with the homologies and inter-relations of the various categories of sex conditions and structures. Whatever may be the basis for the various hypotheses of sex in *Drosophila* and other advanced animal species with rather constant individual sex conditions these hypotheses can refer to only a very small fraction of the sex conditions present in both plants and animals and are not to be applied as generalizations, as many under the spell of the *Drosophila* obsession are inclined to do.

The following observations and experiments on sex expression in various plants in relation to heredity and environment give further evidence on the nature of sexuality and sex as physiological phenomena. Apparently many of those who deal with the problem of sex are unacquainted with the homologies and differences existing between the sexual conditions and structures of the gametophytes and sporophytes of higher plants. It is an absolutely established fact that the maleness or femaleness of the gametophytes of the heterosporous plants never depends in any way on the segregation of hereditary factors nor even in the slightest degree on an allosome differential which may be present after the reduction division. The unisexuality of the gametophyte of heterosporous plants is always determined by the physiological, sexual state of the tissue from which the sporocytes and spores are derived, whether the sporophytes are monosporangiate or bisporangiate, whether they contain allosomes or not. It must be emphasized that there is never any segregation of chromosomes or genes in the heterosporous plants which has any influence whatever in determining the gametophytic sex conditions. This fact is in itself a proof that sex determination is primarily physiological. In view of this condition of things, it is remarkable that many genetecists still seem to think that the unisexuality of the sporophyte must be brought about by a fundamentally different biological process, namely by some hereditary differential. But most sporophytes are hermaphrodites in respect to sex condition and in both the monecious plants and those with bisporangiate flowers the sex of the given part or tissue is determined by physiological states. It is also well to remember

[1] Papers from the Department of Botany, The Ohio State University, No. 354.

that the unisexual gametophytes of heterosporous plants not only show the most extreme sex dimorphism but also the greatest stability of their sexual states of any organisms whether plant or animal. It is in the unisexual sporophytes where sex reversal is often easily accomplished. In those cases where allosomes are present the male gametophytes which contain the "female determining" chromosome retain a constant male state and produce spermatozoids without exception as definitely as their brother male gametophytes do which contain the "male determining" chromosomes. It seems reasonable to demand that those who deal with such a fundamental potentiality as sexuality be acquainted with as much plant morphology at least as is now usually taught in the general elementary botanical course.

CHANGE OF SEX CONDITIONS IN THALICTRUM DASYCARPUM FISCH. AND LALL.

In 1919, the writer published some observations on the nature of the diecious condition in *Thalictrum dasycarpum* and in 1923, he published evidence of definite sex reversal in both directions in this species and also evidence of instability in *Thalictrum dioicum* L. In 1925, the results of further experiments on these two species were published, establishing the fact that the sexual condition can be changed from year to year. In the meantime, Kuhn has made extensive observations on a number of species, studying the chromosome conditions and carrying on breeding and hybridization experiments. All of these studies go to show that *Thalictrum* is a very suitable genus for the study of dieciousness and sex conditions in general.

In 1931, the writer began a new series of observations and experiments on *Thalictrum dasycarpum* in order to determine more definitely the stability or instability of the individuals in respect to their sexual expression. The genus *Thalictrum* belongs to a family near the base of the dicotyls and exhibits, as numerous other genera both low and high in the phylogenetic scale, a rather close gradation of species from those with typical bisporangiate flowers with no indication of a diecious nature to species which are strongly diecious both in the distinctness of the sex individuals and the constancy of the given male and female conditions. *Thalictrum* is interesting among diecious angiosperms in that no vestiges of the opposite sporophylls are present, the sporophylls all developing as normal stamens and carpels except in the special cases of sex-reversal of individual flowers when the sporophylls may be of any degree of perfection or imperfection. This flower condition corresponds to the monecious and diecious flowers of the gymnosperms where usually no opposite sporophyll vestiges are present except in the highly specialized Gneteae.

A study of the sex expression of the various branches on the same shoot of intermediate plants was made and these differences, as will appear below, correspond to the differences between entire annual shoots from the same crown or the differences which may develop from year to year. Out of a large number of carpellate shoots, gathered from their native habitats, studied statistically a few representative examples are presented below. Shoot No. 1 had ten branches with pure carpellate flowers and one branch had one flower with stamens among many pure carpellate flowers. No. 2 had one branch with pure carpellate flowers and five branches each with one flower containing stamens among the carpellate flowers. No. 3 had twelve branches with all pure carpellate flowers and five branches had each one flower with stamens among the carpellate flowers. No. 4 had four branches with all pure carpellate flowers, five branches each with one flower with stamens, one branch with three flowers with stamens, and one branch with four flowers with stamens among the carpellate flowers. No. 5 had four branches with all pure carpellate flowers, four branches each with one flower with stamens, one branch with three flowers with stamens, one branch with four flowers with stamens, two branches each with five flowers with stamens, one branch with six flowers with stamens, and one branch with seven flowers with stamens, among the carpellate flowers. No. 7 had one branch with all pure carpellate flowers, three branches each with one flower with stamens, seven branches each with two flowers with stamens, one branch with eight flowers with stamens, two branches each with nine flowers with stamens, and one branch with ten flowers with stamens among the carpellate flowers. No. 10 had two branches with all pure carpellate flowers, one branch with one flower with stamens, two branches each with two flowers with stamens, two branches each with three flowers with stamens, two branches each with four flowers with stamens, one branch with five flowers with stamens, one branch with six flowers with stamens, one branch with seven flowers with stamens, one branch with eleven flowers with stamens, one branch with twelve flowers with stamens, and one branch with sixteen flowers with stamens among the carpellate flowers.

In Northern Minnesota an interesting intermediate plant was found, in 1934, in which all the flowers were typically bisporangiate with the stamens below and the carpels above. Just beside this plant were some individuals with slight sex reversal and some pure carpellate and staminate plants.

In 1931 also, thirteen plants were transplanted from their native habitat of partly shaded, rich, alluvial soil to an exposed, rather sterile and rocky, clay soil. These plants had the following sex expressions in 1931.

Nos. 1 and 2 were of mixed sex expression; decidedly carpellate with some staminate development.

No. 3. Mixed sex expression; staminate with some carpel development.

Nos. 4, 5, 6, pure carpellate.

Nos. 7, 8, 9, 10, 11, 12, 13, pure staminate.

The plants developed no flowers in 1932 but made a good growth. In 1933 the flower development was as follows:

Plant No. 1 remained decidedly carpellate, but with some bisporangiate flowers, each with one to several stamens.

Plant No. 2, had three shoots. The first and largest was pure carpellate in expression, the second had nearly all the flowers bisporangiate, while the third was prevailing carpellate but with numerous flowers showing one or more good stamens.

No. 3 had six shoots all decidedly staminate but each had several flowers with some carpels.

No. 4 had two shoots strongly carpellate and each had a flower with one good stamen and a second flower with an imperfectly developed stamen.

No. 5 was strongly carpellate but each of its three shoots had several flowers with one or more good stamens.

No. 6 had two shoots, both pure carpellate.

No. 7 had six shoots; three shoots had each several flowers with one or two good carpels among the staminate flowers; one flower had three good carpels; the other three shoots of this plant were all pure staminate.

No. 8 had several flowers with one carpel each.

Nos. 9, 10 and 11 were pure staminate.

No. 12 had a great number of typical staminate flowers and several flowers with one or two imperfectly developed carpels; one flower had one good carpel.

No. 13 was prevailingly staminate but with a considerable number of bisporangiate flowers each with one or more good carpels.

Thus in two years after a change in habitat, of the three originally pure carpellate plants two developed some maleness and one remained pure female; and of the seven plants originally pure staminate four showed some reversal to femaleness and three continued pure male expression.

Since the ground was very sterile, the plants received an application of manure in 1933. This increased the vigor of growth decidedly but apparently had no special effect on the subsequent sex expression. In 1934, the thirteen individuals had the following sex conditions:

Plant No. 1 was small and did not bloom.

Plant No. 2 had seven flowering shoots; one shoot had a mixture of

pure staminate, pure carpellate, and bisporangiate flowers, the latter ranging all the way from having one member of the opposite sex to flowers with about an equal number of stamens and carpels; one shoot was mostly carpellate but had one stamen; the other five shoots had all pure carpellate flowers.

No. 3 had three flowering shoots; two shoots were staminate with some carpel development; the other shoot, which was the largest, was decidedly carpellate with numerous pure carpellate flowers but with some bisporangiate flowers and two pure staminate flowers.

No. 4 had developed four flowering shoots; one was carpellate but had one bisporangiate flower with one good pollen-producing stamen; the second was carpellate but with three bisporangiate flowers, each with one good pollen-producing stamen; the third shoot was also prevailingly carpellate but with two bisporangiate flowers each with one stamen and one of them with a carpel-stamen mosaic additional; the fourth shoot, which was the smallest, was pure carpellate.

No. 5 had two flowering shoots, both pure carpellate.

No. 6 had two flowering shoots, the one was pure carpellate and the other was carpellate but with one flower with an imperfectly developed stamen.

No. 7 had nine flowering shoots; two shoots had only pure staminate flowers; four shoots had some pure staminate flowers and each of them also had a number of decidedly carpellate flowers but with one or more stamens; the seventh shoot was decidedly carpellate, about half of the flowers having one or more carpels, the eighth shoot was extremely carpellate, developing more carpels than stamens, with only four pure staminate flowers among over 100 carpellate ones which produced good seed; the ninth shoot was small and produced about as many stamens as carpels mostly in bisporangiate flowers.

No. 8 had six shoots, five of which were pure staminate and one with mixed sex expression, having thirty pure staminate flowers, sixteen bisporangiate flowers with 1–12 carpels each and one pure carpellate flower.

No. 9 had four flowering shoots all pure staminate.

No. 10 had three flowering shoots all pure staminate.

No. 11 had five flowering shoots, four pure staminate, and one staminate but with two flowers each with an imperfectly developed carpel.

No. 12 had five flowering shoots all pure staminate.

No. 13 had four flowering shoots of which three were pure staminate and one was staminate but with a flower containing an imperfectly developed carpel.

From the above record, it appears that there is the same diversity in

sex expression in individual plants from year to year and in the individual annual shoots developed from the same plant as there is between the main branches of a single bisporangiate shoot, as determined by statistical methods on plants growing in their original habitats.

Of the three originally pure carpellate plants (Nos. 4, 5, 6,) all changed to intermediate sex expression altho one showed only the slightest trace of sex reversal. Plant No. 4 developed some stamens in both 1933 and 1934. Plant No. 5 showed mixed expression in 1933 but was pure female again in 1934. Plant No. 6 remained pure female in 1933 but developed a single imperfect stamen in 1934. Thus all three showed the presence of both male and female potentiality altho in general the expression was decidedly female. Of the seven originally pure staminate plants (Nos. 7, 8, 9, 10, 11, 12, 13,), five showed some reversal to femaleness and two remained pure male for the period of four years. Of the three originally bisporangiate plants (Nos. 1, 2, 3), No. 1 remained practically unchanged, continuing a carpellate-staminate sex expression. Plant No. 2 showed decided sex disturbances, producing a pure carpellate shoot in 1933 along with 2 bisporangiate shoots. Plant No. 3, which was originally staminate-carpellate with a preponderance of staminate expression remained about the same in 1933, while in 1934, of its three developed shoots, two were decidedly staminate and one was decidedly carpellate. It had changed from a predominantly male reaction to a predominantly female reaction. The most decided change in sex reaction was shown by plant No. 7 which changed progressively from a pure male reaction to a decidedly female reaction with hundreds of good fruits in 1934. (Fig. 1)

As a result of these observations it is evident that in a diecious plant like *Thalictrum dasycarpum*, every cell has a bisexual potentiality as the writer and others have maintained and as Kuhn has recently stated. The hereditary factors which cause dieciousness are not a set of male and female segregating and aggregating genes, but rather an accumulation of new potentialities in the protoplast with an originally bisporangiate potentiality. These potentialities, with a given internal or external condition, cause a physiological balance in the egg or zygote, or in the vegetative cells, before, at the time of, or after fertilization, of such a nature that the sex balance swings, for the time being, toward female (+) or male (−). Furthermore, there are potentialities evolved, in passing from the bisporangiate flower condition to the diecious state, which determine or condition both the degree of intensity and fixity of the sex differentation. It has been found from a taxonomic study that the presence or absence of vestiges of the opposite sporophylls in a flower are no criterion for determining the fixity of the sexual states. These physiological potentialities,

in *Thalictrum* and a great number of other genera, form a closely graded orthogenetic series, giving a large number of types of dieciousness in respect to the fixity of the male and female states and the percentage of intermediates or bisporangiate individuals usually appearing in their native habitats.

URTICASTRUM DIVARICATUM (L.) KTZ.

Urticastrum divaricatum is a perennial, herbaceous, monecious species which usually grows from one to four feet tall. After attaining some size it begins to produce loose staminate flower clusters in the upper leaf axils and finally at the end of the growing period several carpellate flower clusters at the tip of the stem. The carpellate inflorescences are usually arranged in the form of a terminal rosette. After seed production the aerial shoots begin to die down to the ground. Some plants of this wood-nettle were dug up in the forest, in the autumn and planted in large flower pots in the greenhouse. After a period of rest they were brought into activity by means of continuous light and the new shoots soon made a vigorous growth. They were then allowed to grow and bloom normally and the usual sequence of axillary inflorescences appeared. The lower were staminate and at the tip of the stem a number of carpellate inflorescences developed. When well advanced in the blooming period they were vigorously treated for rejuvenation by means of continuous light (two 200 Watt Mazda bulbs) and abundant water. The shoots soon continued a vigorous new growth both in the terminal buds and in some lateral buds. The artificial light was turned off again and since it was now the last of March the plants were getting a continuously longer daily light period. In several weeks inflorescences began to develop and these were again staminate. Thus the normal gradient, which is first neutral, then male, then female, and finally death, was reversed to maleness again. Unfortunately these plants were injured by an attack of the red spider so that the tips were destroyed and the experiment was abandoned. With further development the vegetative axis would, no doubt, have produced carpellate inflorescences again at the culmination of the new gradient.

The sex determination in this plant is dependent on the functional state of the cells involved and this in turn is dependent on a definite gradient of maturity, which the given general hereditary constitution of the plant carries thru in a definite way in the usual ecological conditions in which it grows. In a new ecological world with rejuvenation of the terminal bud, a new reversed gradient in the reproductive condition is established and the sex balance swings from female to male rather than from male to female as in the original sequence. The sex expression does not

remain at the final female level but changes with the changed physiology of the cells concerned. This species is apparently a favorable monecious perennial for carrying on experiments in rejuvenation and the changing of the sex determination in relation to changing physiological states.

ZEA MAYS L. WITHOUT STAMENS

In 1928–30, the writer discovered a method by which the expression of maleness could be completely suppressed in Indian corn, resulting in pure female phenotypes. In a plot of "Narrow-grain Evergreen Sweet" corn planted on Oct. 10, 1928, there were 29 plants and not a single normal stamen was produced by the entire plot. This was such an interesting occurrence that it has been repeated several times since just for the pleasure of seeing the experiment come true. On Nov. 15, 1932 a small plot of "Woodburn Yellow Dent" corn was planted in the greenhouse, in a corner where there was shading of light because of the rafters in the roof. There was thus not only a decreasing photoperiod during the earlier stages of the growth of the plants but the light intensity was also decreased at various intervals of the day. The temperature was the ordinary variable greenhouse temperature and the plants were growing on shallow benches of good soil. The result was essentially the same in this dent corn as in the sweet variety. There were 12 plants in the plot and the terminal inflorescences and side ears were completely developed by March 10, 1933. There was not a stamen in the whole patch! Three plants had completely neutral, rudimentary "tassels" and nine plants had developed "tassels" with more or less female expression. In 1928 a plot of "Early Connecticut" dent corn representing a pure line, inbred for ten generations, had 44 plants. Of these, two plants produced a few stamens and 42 produced no stamens. In this case the photoperiodicity in combination with the temperature and other ecological conditions was not quite perfect, so that only about 95% developed with pure female reproductive expression.

In both monecious and diecious species there are various types of general hereditary constitutions which determine the constancy and direction of sex expression in relation to the ecological-physiological conditions. In *Zea mays* the hereditary balance is so conditioned that with the usual favorable environmental conditions of growth, the ecological light gradient causes the sex balance to swing from monecious expression to pure female expression or vice versa but not to pure male expression. In *Arisaema Dracontium* (L.) Schott. the situation is just the opposite, so that with favorable nutrition and abundant water the sex expression is completely monecious while with poor soil and dryness the expression is completely male. The sex-balance swings from moneciousness to maleness or

vice versa but rarely if ever to pure femaleness. In *Arisaema triphyllum* (L.) Torr. there is an equally balanced diecious condition so that the sex-balance swings from male thru moneciousness to female or from female thru moneciousness to male. In *Cannabis sativa* L. there is an equal sex-balance so that the change from femaleness to maleness or from maleness to femaleness is brought about with equal readiness and with this odd situation—exactly the same ecological conditioning with the proper photo-period will cause the males to change to female and the females to male expression. In the diecious *Carica papaya* L., according to common report, apparently males change readily to females but females have, so far, not been changed to males.

It is evident that all hereditary complexes of the numerous common varieties of Indian corn can be induced, in proper environments, to undergo exactly similar sex reactions, no difference what the gene balance may be, and the similar reactions in respect to sex are initiated by environmental and not by hereditary conditions. Such a condition of things is contrary to Mendelian activity. As Yampolsky has recently stated: "The *n*-number of sex forms refuse to submit themselves to the concept that sex is an alternative kind of inheritance. Neither sex categories nor sex chromosomes hem in the variability of sex expression exhibited by *Mercurialis annua*." Richey and Sprague seem not to have understood the point which Yampolsky, the writer, and others have made when it was insisted that the diversity of sexual expressions does not correspond to a gene differential. The diversity of expression in the individual species or variety was always the point at issue. The main question is as to what causes various individuals of the same species or variety to have diverse sexual characteristics for the time being and what causes an individual to have different sexual expressions from year to year or from time to time. The attack has been and still is on the mistaken notion that there are allelomorphic male and female genes or determiners.

GENERAL DISCUSSION OF PROBLEMS RAISED BY THE EXPERIMENTS

With the acceptance of a physiological theory of sexuality and sex, and the abandonment of the sex gene hypothesis all the known morphological and physiological conditions of gametophytes and sporophytes and of hermaphroditism and unisexuality fall into a harmonious agreement. Some, however, still believe that the presence of allosomes points to a genetic explanation. But when we remember that all the fundamental characteristics of sexuality, even including unisexuality, were evolved before the appearance of segregative allosomes in the plant kingdom, it becomes much easier to believe that allosomes are the result of the evolution of

one kind of unisexuality rather than the cause. All we need to assume is a differential sex attraction in fertilization which would account for the fact that apparently the A and B allosomes have a definite relation to the two sexes as originally determined in the zygote. After sex reversal has taken place it is found that there is no such relation or rather that the relation is just the opposite from what it is in the original tissues.

Differential attractions, or compatibilities and incompatibilities are general phenomena, in both the plant and animal kingdoms, between gametes of like and unlike hereditary constitutions and are also in evidence in the differential synapsis of chromosomes and in the favorable or less favorable growth of pollen tubes in the ovules and carpels of seed plants. The physiological theory will also tolerate the assumption that some allosomes contain differential physiological factors, which set up differential physiological reactions at the time of fertilization and thus cause the sex balance to swing to the male or female state in the fertilized egg in the way that physiological states are initiated at a later period by ecological conditions and thru which the established sexual state may be completely reversed because the ecological influence is stronger than the assumed physiological determiners in the allosomes; or in the same way as sex is determined in the specific parts of bisporangiate sporophytes.

Diecious plants cannot be distributed into two distinct categories as subdiecious and true diecious, because there is often a close gradation series between the more primitive species with bisporangiate flowers thru various types of dieciousness to the extreme diecious condition. There is also a similar gradation series in the various types of monecious species and in the groups ranging from ordinary moneciousness to extreme dieciousness. The fact that some diecious species will readily change their sexual states in a given ecological condition while others do not has nothing to do directly with the *time* when the original determination took place. The intensity of the given physiological differentiation and its reversal are different phenomena from that which initiated the state in the first place and determined the dieciousness.

Correns' empirical formula for sex determination and inheritance, with its four general types of sex, its gene complexes, G, A, Z, and "Realizators" having varying valences, is only a fantastic thought pattern which does not at all agree with the known complexity and nature of the types of bisporangiate and diecious conditions present in the sporophyte of seed plants and the sex conditions shown by their gametophytes, nor the neuter conditions of the sporophytes of the homosporous plants and the various sex conditions of their gametophytes. The numerous ecological experiments on sex reversal in both monecious and diecious species as well as

the reversals accomplished in the lower types of gametophytes are all in agreement with the deductions to be made from an evolutionary and taxonomic study of plants and are also in accord with a correct genetic interpretation, namely when genetics is interpreted in terms not only of genes but also in terms of character expression thru the determination of physiological and ecological conditions and ontogenetic gradients.

The bisporangiate flowers also show a large number of types of hereditary expression, in respect to sex, comparable to the several types of monecious inflorescences. This is especially prominent in the lowest types of angiosperms with long floral axes. In the angiospermous bisporangiate flowers, if no disturbance, like dieciousness or moneciousness, has been introduced, the sex balance almost invariably proceeds from the neutral condition to the male condition to the female condition. Now in various species the growing bud may stay but a very short period in the male state and a long time in the female state so that the result is a flower with few stamens and very numerous carpels. Or the heredity may be just the opposite, giving a flower with many stamens and very few carpels. In other cases there are constantly as many stamens as carpels. Now these bisporangiate flowers are apparently much less subject to sex changes than either monecious or diecious types. The gradients seem to move at a very definite rate, altho in nature one occasionally finds a disturbance. It seems reasonable that the point of sex reversal on the floral axis might be shifted by employing suitable ecological conditions even tho the axis and time of its growth are very short when compared with the axes of the inflorescence of the monecious plants or the entire axis of a diecious species.

Sex determination is just as definite and just as decided in the more extreme types of monecious plants as in the diecious species, and constancy of the sexual states in the monecious branches and bisporangiate flowers is just as pronounced. Since we know that in the case of monecious plants, plants with bisporangiate flowers, and hermaphroditic gametophytes there is no shifting of chromosomes and no segregation of heredity, the physiological theory of sex determination is the only one to be entertained.

Some geneticists have been inclined to compare the universal sex dimorphisms and trimorphisms with specific dimorphisms arising in the ontogenetic development of an organism. Thus Emerson, in 1924, asked: "Is the association of pistils and stamens in a single flower either more or less mysterious than the differentiation of the aleurone layer from the rest of the endosperm?" This comparison however is beside the point. In a monecious plant the vegetative tissues in the respective male and female states,

as leaves and stems, show the same physiological differences as are shown by the stamens and carpels. But aleurone and non-aleurone layers have physiological and chemical differences not found in the leaves or stems of a corn plant. In sexuality we have male, female, and neuter conditions and these are general phenomena in the plant and animal kingdoms. But specific heredities due to Mendelian factors or more general potentialities are of an entirely different nature. An earthworm has both ovaries and spermaries in which ova and spermatozoa are produced and a stalk of corn also has ovaries and spermaries in which eggs and sperms are produced and these have the same general properties and reactions in either case. But an earthworm has neither endosperm nor aleurone layer.

Camp has recently shown by conclusive physiological-chemical tests that the male and female tissues of a monecious plant are just as definitely distinct as in a diecious species; and it must be remembered that in either case all the cells of a general male or female system show the given reaction and not merely the cells concerned directly with reproduction.

A fundamental theory of sex must then, among other things, take account of the evolution of the time of sex determination in the ontogenetic cycle as expressed in a given environment, the degree of intensity to which the given physiological state or reaction is developed at various stages of the ontogeny, also in relation to environment, and the readiness with which a given sexual state can be reversed from time to time in the life of the individual, whether it was originally determined in a vegetative tissue or in the zygote at the time of fertilization. We know from the action of haploid sporophytes and diploid gametophytes, when compared with their normal alternate generations, as diploid fern gametophytes for example, that the indications as to the nature of the hereditary units concerned are quite different in the gametophyte from what they are in the sporophyte in respect to sex as well as to other characters, altho they have in this case exactly the same chromosome complement and the same hereditary constitution.

SUMMARY

1. Both staminate and carpellate plants of the diecious *Thalictrum dasycarpum* underwent sex reversal in varying degrees when transplanted to a different habitat and the extent of the reversal was in some cases decidedly different in different years.

2. Shoots of the monecious *Urticastrum divaricatum*, after having produced the regular succession of staminate and carpellate inflorescences, on being rejuvenated by means of a continuous daily photoperiod, reversed from carpellate to staminate development.

3. A plot of "Woodburn Yellow Dent" *Zea Mays*, developed in the greenhouse with a short daily photoperiod and consisting of twelve individuals, showed only female development, there being a complete absence of stamens and normal male expression.

4. The experiments indicate that any sexual condition of an individual is not determined by Mendelian sex genes but by a physiological balance which is produced thru the interaction of the general hereditary potentialities of the cell on the one hand and the environmental conditions on the other. There are no sex genes as such and the gametophytes of heterosporous plants show that there are no sex producing or determining chromosomes, whether autosomes or allosomes, since the sex of the gametophytes and their gametes does not correspond to any special chromosome complement but always continues the condition previously determined in the gametophyte. The term "sex chromosome" is an extreme perversion of language and should not be tolerated.

5. The sexual conditions of the higher sporophytes may change from time to time in the individual and thus the sex present for the time is no criterion for determining the actual hereditary constitution in which the sex is being expressed: and it is evident from experimental data that all monecious and diecious species are finally amenable to sex changes thru the proper ecological influences.

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Fig. 1. *Thalictrum dasycarpum*. Abundantly fruiting shoot of plant which three years earlier was pure staminate.

Duplications in Zephyranthes

H. Harold Hume

Studies of plants placed in the genus *Zephyranthes* Herb., *Atamosco* Adans., have been made by Herbert (1837), Roemer (1847), Kunth (1847), and Baker (1888). These botanists discussed all species known to them at the times they wrote. Certain species now included in the genus were placed by Herbert, Roemer and Kunth in other genera. Holmberg (1905) wrote on *Zephyranthes* but limited his treatment of the genus to species, native and introduced, growing in Argentina. Since Baker's study of the group in which he described thirty-four species there has been no comprehensive examination of the genus and in the meantime about thirty plants believed to be specifically distinct have been added by various botanists. It is apparent that a careful comparative study of some of these additions has not been made. The necessity for such a study may be indicated by the fact that while the first listing of *Zephyranthes* in Index Kewensis (1894) gave fifty-one names that had been applied to supposedly different plants, only about fifty percent of them were regarded as valid. What was true of species included in the genus prior to that date is true in some measure of those added by description and publication subsequently.

How many of these may be identical with older species cannot be determined readily and a decision as to their exact status, in many instances, must await further study. While much may be determined by checking more recently described species against such herbarium specimens and illustrations of older described forms as are available, it may be pointed out that final dispositions must wait in some instances upon the examination of flowering plants in their native haunts or preferably upon comparative studies of living specimens grown under the same cultural conditions from seeds or bulbs of known origin. This is of course a difficult undertaking, but certain characters of these plants often are not presented satisfactorily in herbarium material and morphological characters cannot be determined readily without destroying specimens. Thus far a number of species have been studied from herbarium sheets, original descriptions, illustrations and living plants, and it has been determined that at least three duplications have been made. By the same method it has been found that a fourth species, dropped from the genus because it was regarded as a duplication, should be reinstated as proposed by Urban.

Z. citrina Baker and *Z. Eggersiana* Urb.

Baker (1882) described a yellow species, *Zephyranthes citrina*, and stated that his first knowledge of the plant had been gained from a speci-

men in flower furnished by Messrs. Veitch, Chelsea, England, and believed by them to have come from Demerara (British Guiana). The illustration accompanying Baker's description shows the tips of the spathe lacking. In this respect the drawing does not properly represent the plant and the description also is vague on this point. As a matter of fact, the spathe, as in other species, extends beyond the cylindrical portion and terminates normally in two points. The spathe is membranous in *Z. citrina* and quite apparently its upper portion was broken off or removed in some manner before the drawing was made. It also appears probable that this illustration represents two aspects of the same flower. Urban (1907) basing his conclusions upon specimens of a yellow-flowered plant collected in Cuba (Van Herman No. 803) and Haiti (Eggers No. 2634) described *Zephyranthes Eggersiana* n. sp., and referred particularly to the spathe characters presented by Baker as being different from those found in his species. After studying flowering plants produced from bulbs received from British Guiana, unnamed, and Trinidad, labeled *Z. Eggersiana*, an herbarium specimen collected by Van Herman (No. 803) and collections by others, the original descriptions, and the Baker illustration the conclusion is reached that *Z. Eggersiana* Urban is identical with *Z. citrina* Baker. It is difficult to say where this plant is native but with the knowledge now in hand it can be referred provisionally to British Guiana and possibly Trinidad. Juan T. Roig in a letter (now in the New York Botanical Garden Herbarium) to N. L. Britton expresses his belief that this plant is not native in Cuba.

Z. carinata Herb. and *Z. Tsouii* Hu

There grows in Mexico, a large pink-flowered plant that Herbert (1825) described as *Zephyranthes carinata*. Its native home is authenticated by specimens in various herbaria. It is widely distributed and cultivated as a garden plant in the warmer sections of the world. Recently, Hu (1927) described *Zephyranthes Tsouii* n. sp. from Chekiang Province, China. Careful comparison of his description with that of *Z. carinata* by Herbert and a study of the Hu sketch, living plants and herbarium specimens leave no question that *Z. Tsouii* and *Z. carinata* are identical. As already stated, the latter is widely distributed. Bulbs of *Z. carinata* have been imported from Japan, grown and flowered, and in the Gray Herbarium, Harvard, there is a specimen collected at Yokohama by Maximowicz as long ago as 1862. It is apparent, therefore, that this species has been in the Orient for many years. In the Hu illustration the impression is of a flower with pointed sepals and petals. This is only apparent because their margins are rolled inward as they normally are in flowers just opening. Moreover

4-merous development, five stigmas and other abnormalities are so frequent in *Z. carinata* as to be almost characteristic. Neither capsules nor seeds are illustrated or described and so far as known the species very rarely or never forms seed. Indeed it may be a clon, perhaps a hybrid.

Z. robusta (Herb.) Baker and *Z. Taubertiana* Harms

Zephyranthes robusta (Herb.) Baker dates back more than a century to the time when Herbert (1829) described it as *Habranthus robustus*. Baker (1888) transferred it to *Zephyranthes*. It has been illustrated by Herbert (1829), Loddiges (1831) and Stapf (1927). On the whole these illustrations are good and sufficient for identification of the plant. Its general characters are such as to separate it readily from most other species in the genus. It has large, light pink, declinate flowers and is a valuable ornamental. Harms (1895) described *Zephyranthes Taubertiana* as a new species from a pot-grown plant without stating where it was native, and later published an illustration and a popular description (1896). Careful comparison of available illustrations and descriptions and study of living plants show that *Zephyranthes robusta* and *Zephyranthes Taubertiana* are names applied to the same species and the latter becomes a synonym.

Z. bifolia (Aub.) Roemer and *Z. rosea* Lind.

The status of the West Indian *Zephyranthes bifolia* has been in doubt for many years, the name having been regarded as a synonym of *Z. rosea*. It is so listed in the Index Kewensis (1894) and because of lack of detail in the first and for many years the only description its identity and validity have been questioned. Scant diagnosis of species, lacking in important details, are not unusual among the earlier descriptions of plants belonging to this genus.

The botanical history of *Z. bifolia* begins with a drawing (No. 147) by Plumier of a plant credited to Santo Domingo and Cayenne. This drawing is labeled *Lilio-narcissus bifolius purpureus*. Through the kindness of Professor H. Humbert a photograph of the Plumier illustration, in the Museum National d'Histoire Naturelle, Paris, France, is in hand. It represents a species of *Zephyranthes*. Two views of the same bulb in bloom are shown to bring out the inner and outer characters of the flower. The leaves taper to a sharp point and the longer one exceeds the scape. The peduncle is of medium length. The spathe is longer than the peduncle with the points of its divisions extending above the ovary. The tube is short, and the perianth parts are broadly oval, rounded to their apices. The stigmas extend beyond the anthers.

With a three word description and reference to Plumier's catalogue

and manuscript, Aublet (1775) established the binomial "*Amaryllis bifolius.*" From the Plumier sketch, Lamarck (1783) described *Amarillis à deux feuilles* at some length. No allowance was made for variations in the plant not brought out in the drawing; indeed, the description fairly covered only what the drawing showed. Herbert (1837) placed the plant as a variety of *Zephyranthes rosea*, apparently without having seen the Plumier drawing. Roemer (1847) listed *Z. bifolia* as a doubtful species while Kunth (1847) followed Herbert and placed it as a variety of *Z. rosea*. Baker (1888) thought it probably was identical with *Z. rosea*. Apparently all descriptions of this plant and comments thereon were based upon Lamarck's diagnosis of Plumier's drawing until Urban (1907) wrote a new description from specimens collected in Haiti by Picarda (No. 1087) and Buch (No. 366 and No. 599). The description by Urban fits the plant illustrated by Plumier. Specimens collected by von Turckheim (No. 3042) are in the New York Botanical Garden and the Gray (Harvard) Herbaria and by Fuertes (No. 139) in the New York Botanical Garden. Additional specimens are in the National Museum Herbarium, Washington, D. C.

There remains no doubt that *Z. bifolia* is a valid species distinct from *Z. rosea*. It is neither a duplication of *Z. rosea* nor is it a variety of that plant. In *Z. rosea* the leaves are recumbent, bright green, relatively broad and short, rounded at their apices. The peduncle is about twice as long as the spathe. The perianth parts are narrower and more tapered than are those of *Z. bifolia*. The latter is a more robust plant with longer leaves and larger flowers.

In connection with these studies, specimens in the Gray (Harvard) and the New York Botanical Garden Herbaria have been studied. I am indebted to Dr. E. D. Merrill, Director, The New York Botanical Garden, for this opportunity. Specimens in the herbarium of the National Museum also have been examined through the courtesy of Dr. W. R. Maxon, Associate Curator. Dr. L. H. Bailey, Ithaca, New York has furnished references and citations. To all of these my appreciation is due.

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Explanation of Figures

Fig. 1. *Zephyranthes citrina* Baker. Grown from British Guiana bulbs. $\times \frac{1}{2}$

Fig. 2 *Zephyranthes carinata* Herb. Native in Mexico; common in southern gardens. $\times \frac{1}{2}$

Fig. 3. *Zephyranthes robusta* (Herb.) Baker. Native in Argentina. $\times \frac{1}{2}$

Fig. 4. *Lilio-narcissus bifolius purpureus.* Plumier mss. 147. Photo by A. Cintract, of the original in Museum Hist. Nat. Paris.

Fig. 5. *Zephyranthes rosea* Lind. Native in Cuba. Specimens grown in Florida. $\times \frac{1}{6}$

Fig. 1

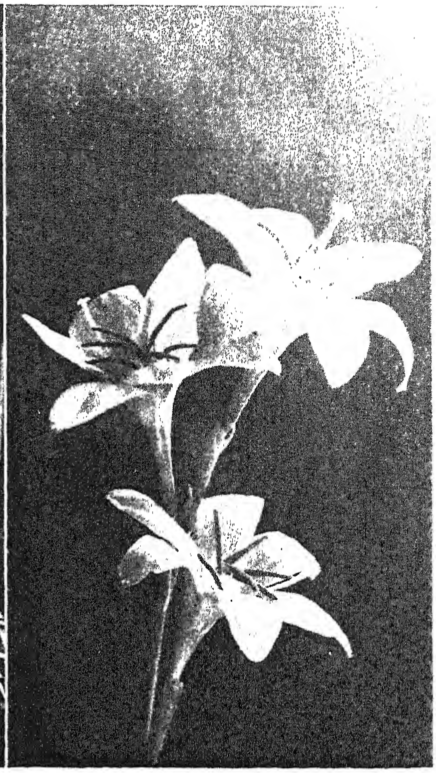

Fig. 2

Fig. 3

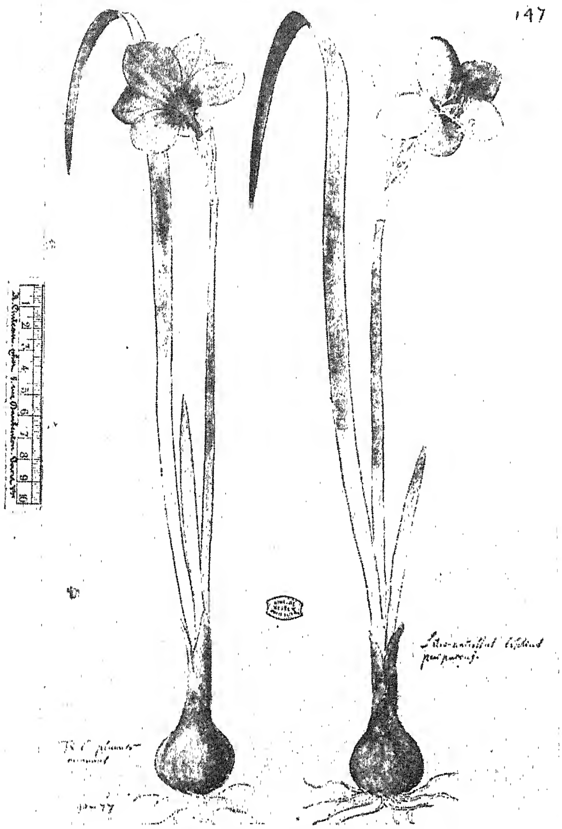

FIG. 4

FIG. 5

The dissociation of Fusarium in soil

C. R. Orton[1]

(with plates 21–24)

The phenomenon in the fungi known variously as "saltation," "variation," "dissociation," "mutation," and "sectoring" has been described by many workers from laboratories throughout the world. The phenomenon is best illustrated by the appearance of sectors of a strikingly different aspect as a colony develops on an agar plate.

Numerous attempts have been made to explain this phenomenon. Some think it may be due to a particular constituent or combination of constituents of the substrate; some have attributed it to hyphal fusions, to "mixochimaera," cytoplasmic inheritance, etc.; by others it has been attributed to high temperatures; and in lieu of any specific evidence many have concluded that "sectoring" is in some way bound up with the artificial culture of these organisms.

While such "dissociants" are well known to vary widely from their parental stocks in both physiologic and pathogenic behavior, few investigations have been made to determine what part these "dissociants" play in the development of new parasitic and saprophytic forms under conditions as they exist in nature. In fact heretofore it has been uncertain whether this phenomenon existed outside the cultural conditions of the laboratory.

The first question to be settled, if possible, is whether dissociation takes place in the soil. The investigations of Sleeth (1934) indicated that it does. He reports two instances of dissociants recovered from plants growing in infested flats, which were identical with dissociants which had appeared previously in laboratory plates from the same strain which was used for inoculating soil in the flats. While this was strong evidence of dissociation in the soil, it was not considered adequate proof for the reason that the flats were open to contamination. It seemed necessary to conduct an experiment which would obviate the possibility of contamination factors and at the same time answer this question. Furthermore it opened the question whether those dissociants actually originated in the soil or whether they may have originated in the seedlings.

[1] Published with the approval of the Director, West Virginia Agricultural Experiment Station, as Scientific Paper No. 148.

I wish to acknowledge my indebtedness to Dr. Bailey Sleeth, Mr. Paul Smith, Miss Genevieve Clulo and Mr. Oliver Orton who have assisted in the culture work. Especially am I indebted to the National Research Council, Division of Biology and Agriculture for the Grant-in-Aid which made it possible to carry out these studies.

METHODS

The set-up of the experiment which began in March, 1933, was as follows: Four pounds of prepared greenhouse soil containing approximately 25 per cent moisture was added to each of 32 Erlenmeyer flasks of 2000 cc. capacity and sterilized in autoclave for one hour periods at 15 pounds pressure on three successive days.

For this experiment four strains of *Fusarium niveum*, two strains of *F. vasinfectum*, and one of *F. tracheiphilum* were selected. These seven strains were grown on rice in petri dishes until the entire mass of rice was well permeated by the fungus. Two petri dish cultures of the same strain were used to inoculate four flasks—one-fourth of each dish to one flask, each flask requiring an amount equal to one-half of the culture in a plate. The culture in each case was well mixed with the soil.

The flasks were closed with rubber stoppers containing two holes plugged with sterilized cotton to allow gas exchange but preventing contamination. Paraffined paper cups were inverted over the flask necks to aid in keeping out dust and other sources of contamination.

Two flasks of each of the seven strains plus uninoculated checks were placed in the greenhouse (unshaded) and a like number in a cold frame outside (shaded).

In August, 1933, sixteen additional flasks were prepared as follows and placed in the greenhouse laboratory in shade:

Flask No.	*Size*	*Amt. Soil*	*Treatment*	*pH after Sterilization*
1a	2000 cc.	1000 gm.	$CaCO_3$, 3 gm.	6.58
1b	"	"	" "	6.77
2a	"	"	" 6 "	7.04
2b	"	"	" "	7.00
3a	"	"	H_2SO_4, 1 cc.	5.00
3b	"	"	" "	5.50
4a	1000 cc.	600 gm.	$Ca(NO_3)_2$, 3 gm.	6.05
4b	"	"	" "	6.06
5a	"	"	KNO_3, 3 "	6.10
5b	"	"	" "	6.06
6a	"	"	Oatmeal, 20 gm.	6.42
6b	"	"	" "	6.45
7a	"	"	Untreated, sterilized	6.40
7b	"	"	" "	6.42
8a	"	"	" not sterilized (uninoculated)	7.17
8b	"	"	" " " "	7.07

The pH was determined by Dr. G. G. Pohlman, using the quinhydrone electrode method.

The *a* series with exception of 8a, was inoculated with *Fusarium niveum*, strain 20, and the *b* series with exception of 8b with *Fusarium vasin-*

fectum, strain 104, by transferring the mycelium and spores of each strain from one 2-weeks old petri plate culture to 200 cc. of sterile water. This inoculum was thoroughly shaken and 10 cc. of the spore and mycelial suspension added to each flask. In this experiment the soil in the flasks was near saturation. The flasks were stoppered and protected like those in the March experiment.

At approximately monthly intervals a sample of the soil was taken from each flask in both experiments and plated on Leonian's modified agar of the following composition:

1 gram potassium acid phosphate
1 gram magnesium sulphate
3 gram proteose peptone
15 gram dextrose
20 gram Bacto-agar in 1000 cc. distilled water

Careful attention was directed to a study of the resulting colonies from which three groupings were made: (1) colonies like the parental strain; (2) colonies unlike the parental strain "colony dissociants"; and (3) colonies of the parental strain showing sectorial dissociation.

DISCUSSION

Particular emphasis is placed upon the second group, which records the number of entire colonies different from the parent. When an entire colony, differing in marked characteristics from the parental type, appeared among the normal colonies on the same plate there appears to be no reasonable doubt that it originated in the soil and could be attributed in no manner to the influence of the culture medium or other ecological factors influencing the plate culture.

The sectorial dissociants recorded under group 3 are not so clearly delimited as to their origin. The visual evidence places their origin in the petri dish, but the fact that they occurred repeatedly from the same flask is some evidence that they originated in the flask. However, this question may be considered unsettled for the present.

In a number of cases these "colony dissociants" were like the sectorial dissociants which appeared both from the soil as recorded in group 3, as well as from stock cultures in the laboratory. (See 11a, 20a, 20b, 104a, 104c).

The data are considered conclusive in showing that several strains of *Fusarium niveum* may dissociate as readily in soil as upon laboratory media. We believe this has a direct relationship to the large number of strains which are distributed in nature throughout our watermelon soils.

TABLE 1

Soil flasks in greenhouse (G) exposed to sun and outside in shaded cold frame (C.F.) for 22 months

STRAIN	ENVIRONMENT	TOTAL COLONIES	(1) LIKE PARENT	(2) UNLIKE PARENT "COLONY DISSOCIANTS"	(3) COLONIES SHOWING SECTORING	DESIGNATION AND DISTRIBUTION OF DISSOCIANTS
5	Greenhouse	450	447	3	0	5a, 5b, 5aa;
5	Cold Frame	450	448	2	0	5b, 5aa;
11	G.	450	427	(a) 3(21)	(a)2(2)	(b)11a(5) 11b(5) 11A1(11): 11a(1) 11c(1)
11	C.F.	450	449	1	0	11b
16	G.	450	448	1(2)	0	16a(2)
16	C.F.	450	449	0	1	16a
20	G.	450	438	3	3(9)	20a(1) 20b(1) 20c(1); 20b(4) 20b(3) 20d1(2)
20	C.F.	450	444	3	3	20T1(1) 20T2(1) 20T3(1); 20a(1) 20d(1) 20a(1) 0
101	G.	450	450	0	0	*F. vasinfectum* from Dr.
101	C.F.	450	450	0	0	V. H. Young
103	G.	450	450	0	0	*F. vasinfectum* from Dr.
103	C.F.	450	450	0	0	C. D. Sherbakoff
105	G.	450	447	0	2(3)	105a(1) 105b(2)
105	C.F.	450	450	0	0	*F. tracheiphilum* from C.D.S.
Checks	G.	0	0	0	0	
Checks	C.F.	0	0	0	0	
Totals	G.	3150	3107	10(29)	7(14)	
	C.F.	3150	3140	6	4	

(a) Figures outside parenthesis record number of distinct dissociants in this class secured throughout the duration of the experiment. Figure inside parenthesis record the number of times such dissociants occurred.

(b) The figures in parenthesis in last column record the number of times each dissociant appeared during the period covered by the experiment. The semicolon separates colony dissociants from sectorial dissociants.

Also it is probable that dissociation is responsible for the variation in pathogenicity of the strains occurring naturally. Otherwise how can we account for the variability in pathogenicity of the dissociants secured by Sleeth? Some of these apparently are identical with sector dissociants produced in stock cultures in the laboratory and which have been tested also for pathogenicity.

There is evidence that some strains are much more stable than others with respect to their tendency to produce dissociants. Two strains, 101 and 103, both of which were from wilted cotton plants and were identified when sent to me as *F. vasinfectum*, produced no dissociants during a period of 22 months. On the other hand strain 104, also *F. vasinfectum* from cot-

TABLE 2

Culture flasks stored in shade in greenhouse laboratory for 17 months

STRAIN	SUPPLEMENTAL TREATMENTS	TOTAL COLONIES	(1) LIKE PARENT	(2) UNLIKE PARENT "COLONY DISSOCIANTS"	(3) COLONIES SHOWING SECTORING	DESIGNATION AND DISTRIBUTION OF DISSOCIANTS
20	Same as 104	960	960	0	0	
104	$CaCO_3$, 3 gm.	120	115	(a)2(5)	0	(b)104a(4) 104c(1)
104	$CaCO_3$, 6 gm.	120	120	0	0	
104	H_2SO_4, 1 gm.	120	118	1(1)	(a)1(1)	104a 104a
104	$Ca(NO_3)_2$, 3 gm.	120	120	0	0	
104	KNO_3, 3 gm.	120	120	0	0	
104	Oatmeal, 20 gm.	120	90	2(20)	4(10)	104a(3) 104c(17); 104a (1) 104b(2); 104b1(1) 104c(6)
104 (ck)	Untreated, Sterilized (inoculated)	120	120	0	0	
Check	Untreated, sterilized (uninoculated)	0	0	0	0	
Totals		1920	1873	5(26)	5(11)	

(a) and (b). See footnote table 1.
Strain 20 = *Fusarium niveum*
Strain 104 = *Fusarium vasinfectum*

ton, has produced two distinct dissociants, 104a and 104c, which have appeared 26 different times in three separate flasks. It appears that stability and instability are characteristic of particular strains and are purely relative judging from the results of studies extending over several years in our laboratory. Some isolants have continued to be stable as long as four years and have then dissociated.

The results show more dissociation in the soil in flasks stored in the greenhouse, where they were exposed for 22 months to intense sunshine and high temperatures, than in the soil in flasks stored in a cold-frame, where they were shaded and subjected only to cool and less fluctuating temperatures. There may be some doubt as to the significance of these differences but they are suggestive of results in Barnes' (1930) laboratory where high temperatures have been reported as inducing "variations."

The results obtained with strain 104 in soil which received supplemental treatments indicate that certain of these treatments may have had some influence upon the production of dissociants. The most outstanding result came from the oatmeal-treated flask, where four distinct dissociants were produced. The check flask produced no dissociants. Possibly the presence of abundant organic matter in the soil may exert some influence.

The substrate in this flask showed pH 6.45. I see no particular significance in the results produced in the flask containing 1 gram H_2SO_4 with pH 5.50. The failure of strain 20 to produce dissociants in the supplemental treatments is not explained. Possibly a continuation of this test over a longer period would have given results. This test was continued only for 17 months in contrast to the 22 months' duration of the other experiment.

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Explanation of plates 21–24

Surface characters were taken from upper surface of 7-day-old colony.

Color characters were taken from the lower surface of colony at same age.

Color references are to Maerz and Paul, Dictionary of Color, McGraw-Hill Book Company, 1930.

Plate 21

5—Surface: smooth; color: plate 44; G1, margin lighter

5a—Surface: thin growth of aerial mycelium; color: plate 10; J2

16—Surface: smooth; color: plate 9; A2

16a—Surface: aerial mycelium cottony, but not thick; color: plate 42; I1

105—Surface: much lilac tinted aerial mycelium, fluffy; color: plate 47; J6

105a—Surface: smooth, tendency towards aerial mycelium; color: center, Plate 47; J9, margin, plate 46; between K2 and L2

Plate 22

104b—Surface: scant, cottony, aerial mycelium; color: plate 47; H2, lighter margin

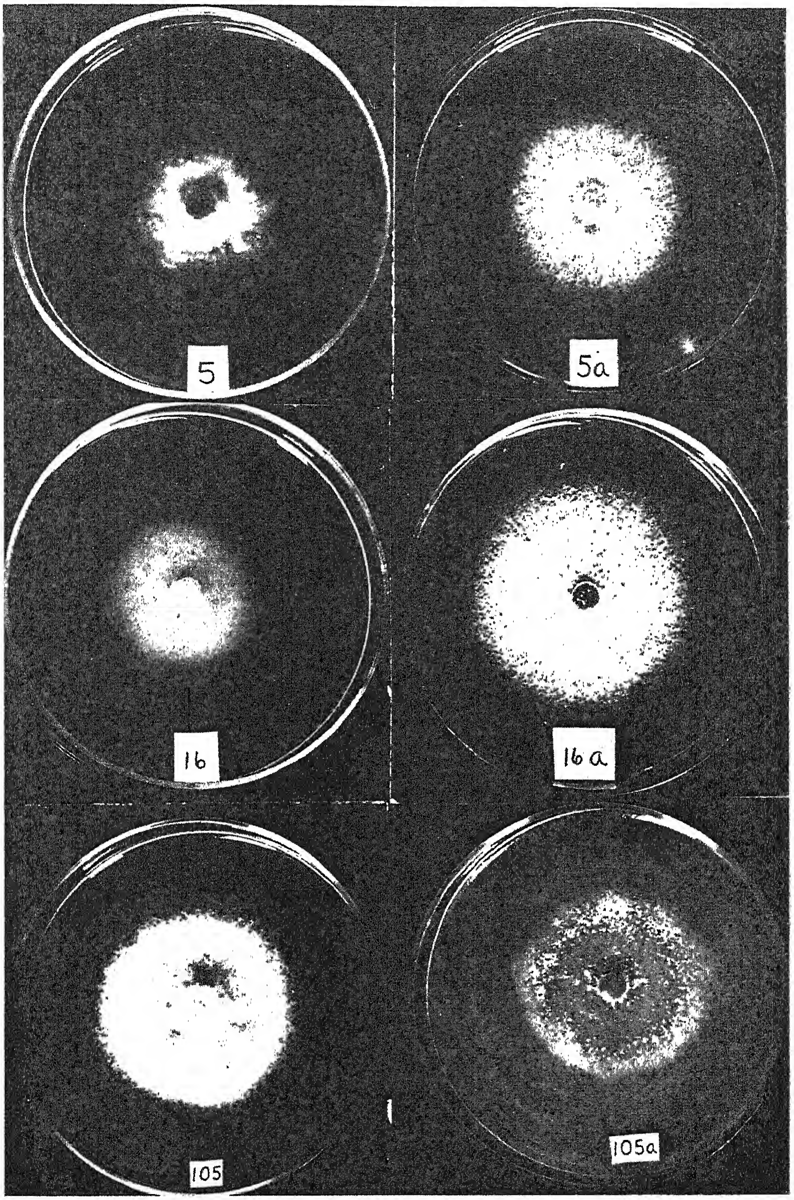
104b1—Surface: good growth of cottony, aerial mycelium; color: plate 48; L12

104c—Surface: much cottony, aerial mycelium, colored; color: plate 47; L8

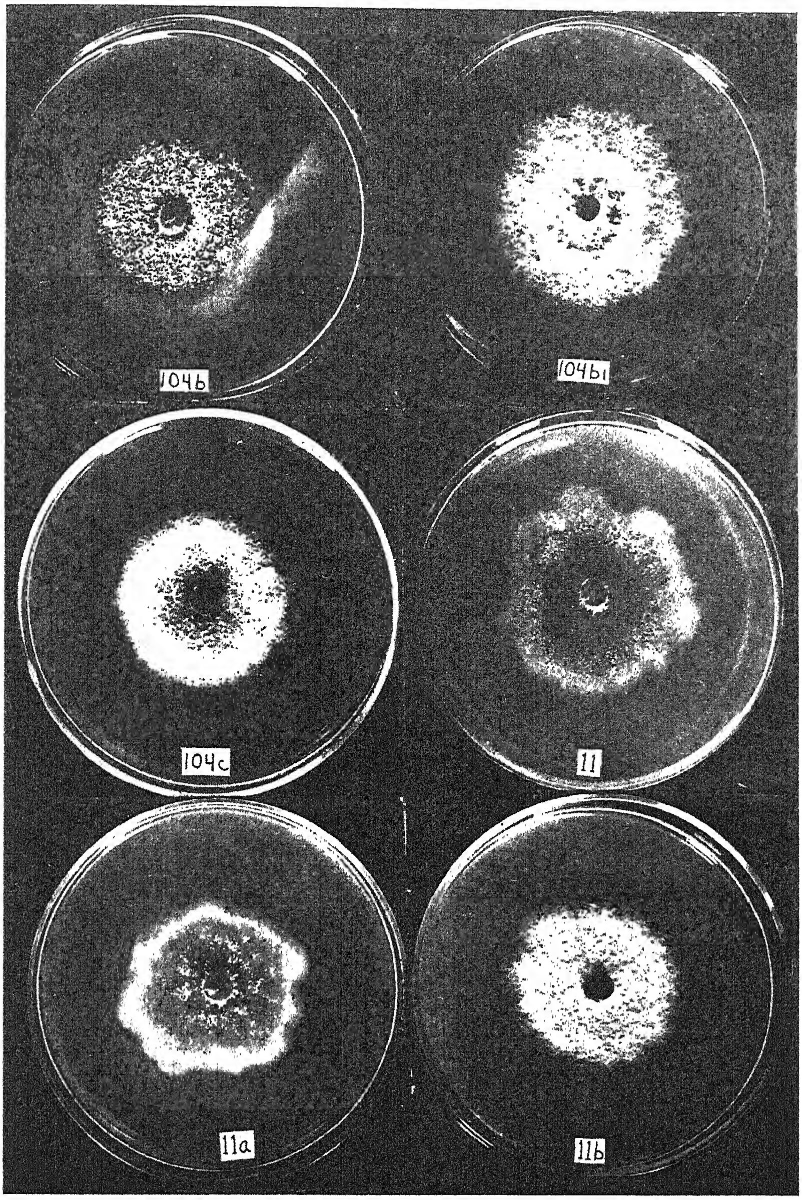
11—Surface: smooth, slight tendency toward aerial mycelium; color: plate 46; between K2 and L2

11a—Surface: smooth, slight tendency toward aerial mycelium; color: plate 47; H5

11b—Surface: small amount of cottony aerial mycelium; color: plate 48; L3



ORTON: FUSARIUM



ORTON FUSARIUM

Plate 23

20—Surface: scant aerial mycelium; color: plate 48; L1, lighter margins, striations present

20a—Surface: good, cottony growth of aerial mycelium; color: plate 48; H12, margins lighter

20b—Surface: luxuriant, fluffy, aerial mycelium, tinted pink near the center; color: plate 47; J3 at center, plate 5; E3 at margins, striations present

20c—Surface: aerial mycelium scant, matted; color: plate 48; L1, faint striations present

20d—Surface: smooth; color: plate 43; F1

20d1—Surface: cottony aerial mycelium, colored near center; color: plate 47; L5

Plate 24

20T1—Surface: scant, cottony, aerial mycelium; color: plate 48; L1, lighter margins, striations present

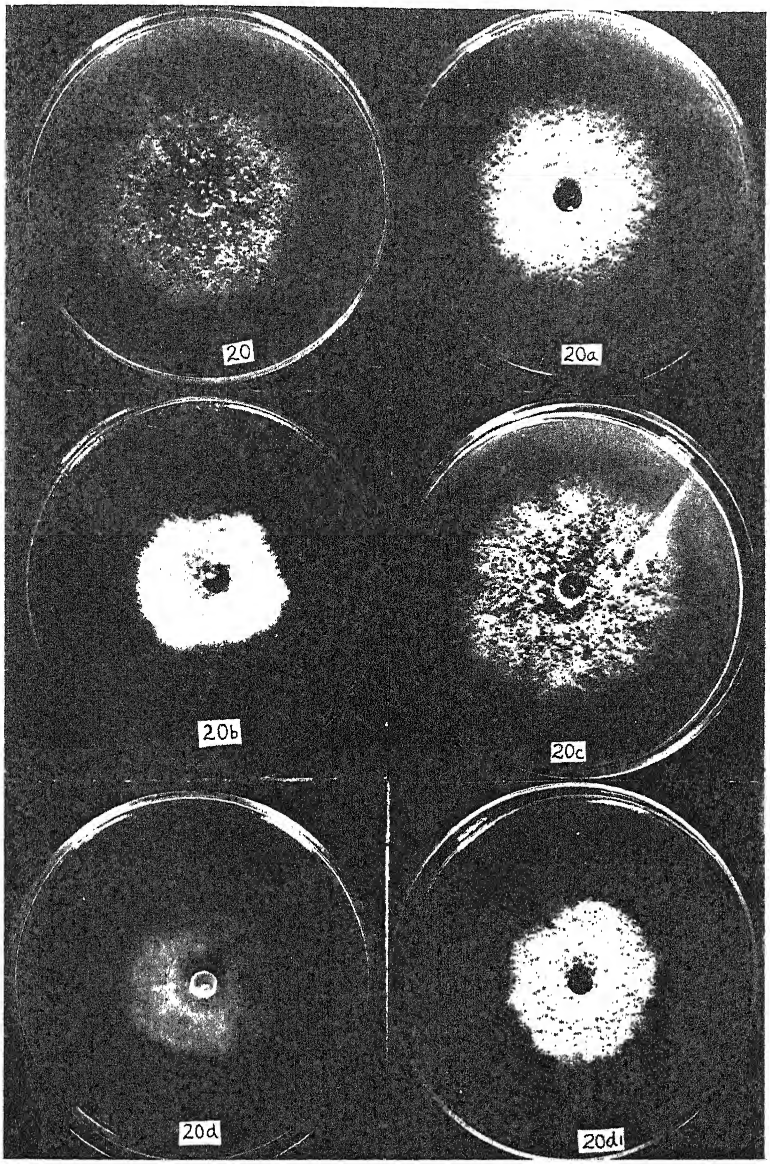
20T2—Surface: smooth; color: plate 43; E1

20T3—Surface: nearly smooth, with a slight tendency towards aerial mycelium; color: plate 46; I1

$\frac{20a}{0}$—Surface: thick, close growth of aerial mycelium; color: white

104—Surface: fine growth of cottony mycelium; color: plate 43; E1

104a—Surface: cottonv aerial mycelium; color: plate 47; J6



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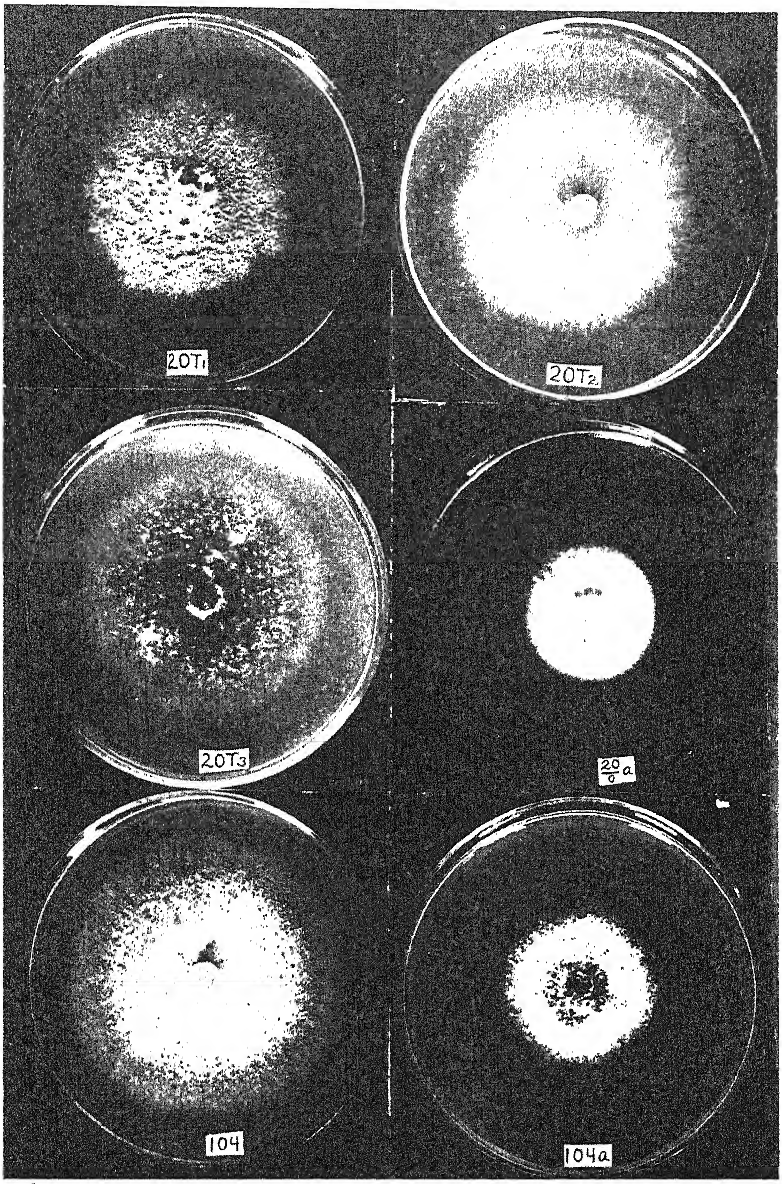

ORTON FUSARIUM

INDEX TO AMERICAN BOTANICAL LITERATURE

1931–1935

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The factors governing shape and size in Capsicum fruits; a genetic and developmental analysis[1]

SAMUEL KAISER

(WITH SEVEN FIGURES)

INTRODUCTION

Living things, and the parts which constitute them, are generally characterized by a definite form and magnitude, capable of relatively slight modification by a varying environment. The diversity of shape and size among plant and animal groups, and the relative constancy of these features within a species or variety, indicate that these characteristics have a definite genetic basis. This has been proved experimentally in a number of cases. In most of these, shape and size seem to be inherited as are most quantitative characters and governed by the action of multiple factors, but in several instances it has been shown that each may be controlled primarily by the action of single genes.

An attempt is made in the present paper to ascertain the genetic mechanism of shape and size determination in the fruits of *Capsicum annuum*. The problem has previously been studied, with results which seem to the writer to be inconclusive. Webber (1912) has reported a cross involving parental fruit types of different size in which the F_1 was intermediate and the F_2 distribution was continuous, being skewed toward the large end. Ikeno (1913) obtained an intermediate F_1 in such a cross also and found in the F_2 a graded series ranging from the size of the large parent on the one side to that of the small parent on the other. His results indicate that the parents differed in four or five size factors. Halsted (1914, 1915, 1916), however, failed to recover the parental types in an F_2 progeny of 1000 plants, indicating that more size factors were here involved. Shape in his material likewise showed a typical "quantitative" inheritance. Groth (1915), having carried out an extensive investigation on tomato fruits, published a plate of pepper fruits (without accompanying analysis) which shows a wide variety of shape and size types in the F_2. Castle (1923) has used such a plate in support of the thesis that size and shape do not have a simple genetic basis, saying, "It is evident that in these cases length and width of the fruit are affected by numerous independent factors which recombine so as to form a complete series of inter-

[1] Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Faculty of Pure Science, Columbia University, Department of Botany.

[THE BULLETIN FOR OCTOBER (62: 369–432) WAS ISSUED OCTOBER 1, 1935]

grading forms." Dale (1928) has presented evidence for the proportionate effect of a number of quantitative factors controlling fruit length. The most exhaustive study of quantitative characters in this species has recently been made by Deshpande (1933). According to this author, "Length of fruit is probably inherited on a tri-hybrid basis in the ratio of 3 short and intermediate fruits to 1 long." "Thickness of fruit" (the equivalent of width in the present study) "is inherited on a simple monohybrid ratio." With respect to fruit shape, elongate and globose being the contrasted types, "F_1 had partly taken both the characters, one from each parent," and "this character is influenced by a large number of factors." There is thus in this series of findings much that is contradictory. Related work on other organisms will be discussed later in connection with the results obtained from the present investigation.

The analysis which follows will endeavor to establish two main points: (1) that shape and size of *Capsicum* fruits are inherited *as such* and not merely as the resultants of independently inherited linear dimensions, and (2) that the final shape of the mature fruit is genetically determined by the interaction between factors governing the *relative* dimensional growth rates during the course of the organ's development and factors controlling its *absolute* size.

MATERIAL AND METHODS

A number of commercial varieties of the red pepper, *Capsicum annuum*, were inbred for several generations to insure a fairly complete degree of homozygosity, and then crossed. The varieties chosen as parents were those between which there were obvious differences in mature fruit shape and size, and which could be successfully grown in pots in the greenhouse. F_2 generations were grown from several of these. Of the many hybridizations performed four were selected for intensive study, two of which are here reported as examples of two different types. In the cross between Lines VIII and V, the parental fruit types are more strikingly contrasted in shape than in size. The fruits of both types are small. Those of Line VIII are long and narrow, tapering toward the stigmatic end. The fruit is characteristically made up of two carpels and the pericarp is rather thin. At maturity, the placenta bearing the seeds occupies only the basal portion of the berry. In Line V, the fruits are flattened spheres, the apices being blunt. They are usually bicarpellary and the pericarp is thin, but somewhat thicker than in Line VIII. At maturity, the entire berry is filled with seeds. In the cross between Lines IV and IX, the parental fruit types are more extremely contrasted in size than in shape. The mature fruits of Line IV are much larger than those of Line IX and somewhat more

elongate, although not pointed. The number of carpels is variable but is generally two and the pericarp is rather thick and fleshy. Seeds are found only in the basal portions of the mature fruits. Line IX seems to be genetically very similar to, if not identical with, Line V.

Ripe fruits of the parent, F_1 and F_2 plants were measured with vernier calipers and the measurements studied statistically as outlined in the following pages. Length is always measured, in centimeters, as the linear distance from the junction of the ovary base with the receptacle to the ovary-style fusion. Width, in centimeters, is the maximum width of the ovary. The fruits are radially symmetrical, width in all directions being essentially equal. Volume is computed according to the arbitrary calculation width$^2\times$length and is expressed in cubic centimeters. (These computed volumes are obviously larger than the actual volumes; they may be conveniently employed, however, as comparative size values.) Shape index is calculated by dividing the longer of the dimensions by the shorter; but in order to facilitate the statistical work, all the shape indices are expressed

TABLE 1

Summary of statistics in the VIII×V cross. The numbers in parentheses indicate the number of measurements involved.

		VIII (21)	V (60)	VIII×V (36)	F_2 (70)
	$\bar{m}$	6.87±0.09	1.34±0.01	3.74±0.06	4.60±0.10
Length cm.	s.d.	0.64±0.07	0.17±0.01	0.58±0.05	1.28±0.07
	v	9.38±0.99	12.60±0.79	15.37±1.25	27.93±1.71
	$\bar{m}$	1.46±0.03	1.83±0.02	1.75±0.02	2.13±0.03
Width cm.	s.d.	0.18±0.02	0.19±0.01	0.21±0.02	0.36±0.02
	v	12.46±1.32	10.53±0.66	12.21±0.99	17.00±1.00
	r, L-W	+.41± .12	+.67± .05	+.24± .11	−.48± .06
	$\bar{m}$	4.77±0.10	0.73±0.01	2.16±0.04	2.27±0.07
Shape L.	s.d.	0.66±0.07	0.07±0.00	0.37±0.03	0.86±0.05
	v	13.79±1.46	8.95±0.56	17.21±1.41	37.72±2.44
	$\bar{m}$	14.97±0.67	4.59±0.11	11.78±0.40	20.41±0.55
Volume c.c.	s.d.	4.59±0.48	1.31±0.08	3.57±0.28	6.80±0.39
	v	30.64±3.48	28.60±1.90	30.28±2.62	33.30±2.10
	sk				+0.45
	r, S-V	−.45± .12	+.10± .09	−.04± .11	+.03 ±.08
	$\bar{m}$				1.289±.013 (antilog: 19.46)
Volume log.	s.d.				.155±.009
	v				53.63±3.83
	sk				+0.01

in terms of relative length (length divided by width). The advantages of employing shape indices of the former type have been pointed out elsewhere (Sinnott, 1927).

In addition to the study of mature fruit dimensions, those of developing fruits were measured, from young ovaries of .001 c.c. or less in volume to mature fruits of 100 c.c. or larger. This developmental study, which provides a method of analysis not realized by the conventional work with mature fruit dimensions, has an important bearing on genetic interpretations.

STATISTICAL ANALYSIS OF MATURE FRUIT DIMENSIONS

The results of both crosses will be considered together. The frequency distributions for length, width, shape, and volume are given in figures 2, 3, 5, and 6. Summaries of the statistics, including the means ($\bar{m}$), standard deviations (s.d.), coefficients of variability (v) in percent, coefficients of skewness (sk) (for F_2 volumes only) and coefficients of correlation (r)

TABLE 2

Summary of statistics in the IV×IX cross. The numbers in parentheses indicate the number of measurements involved.

		IV (4)	IX (61)	IV×IX (50)	F_2 (105)
	$\bar{m}$	6.28±0.20	1.26±0.02	1.86±0.02	3.39±0.07
Length cm.	s.d.	0.58±0.14	0.20±0.01	0.26±0.02	1.08±0.05
	v	9.25±2.23	16.30±1.02	13.94±0.96	31.98±1.63
	$\bar{m}$	4.48±0.06	1.82±0.02	2.49±0.03	3.53±0.03
Width cm.	s.d.	0.18±0.04	0.23±0.01	0.35±0.02	0.45±0.02
	v	3.99±0.95	12.52±0.78	13.98±0.96	12.84±0.61
	r, L-W	−.27± .31	+.81± .03	+.75± .04	+.16± .06
	$\bar{m}$	1.41±0.05	0.69±0.01	0.75±0.01	0.97±0.02
Shape L.	s.d.	0.15±0.04	0.06±0.00	0.08±0.01	0.32±0.01
	v	10.75±2.59	9.16±0.56	10.15±0.69	32.72±1.68
	$\bar{m}$	125.73±4.38	4.37±0.15	12.08±0.43	43.45±1.22
Volume c.c.	s.d.	12.98±3.10	1.69±0.10	4.52±0.30	18.50±0.86
	v	10.32±2.49	38.59±2.69	37.40±2.85	42.56±2.31
	sk				+3.08
	r, S-V	+.40± .28	+.34± .08	−.13± .09	+.52± .05
	$\bar{m}$				1.599±.013 (antilog: 39.72)
Volume log.	s.d.				.190±.009
	v				31.72±1.61
	sk				−0.26

between length and width, and between shape and volume together with their probable errors, are offered in tables 1 and 2. (The loss of most of

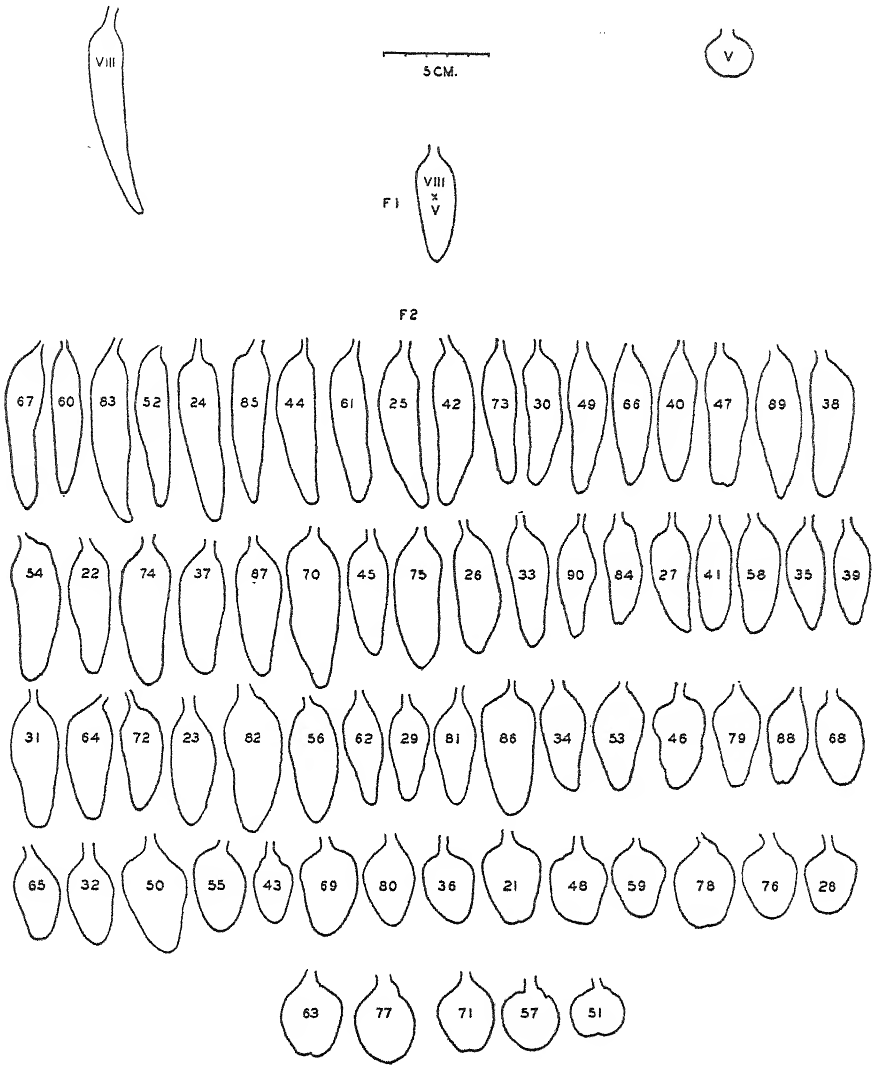

Fig. 1. Trace drawings of typical ripe fruits from the parent plants, VIII and V, the F_1 hybrid between them, VIII × V, and each of the 70 F_2 plants (numbered 21–90) these arranged in a series from the relatively longest to the relatively widest.

No clear segregation in shape is observed.

the ripe fruit measurements for Line IV has made it necessary to work with only four fruits. The statistics based on these, especially the variabilities and correlations, are of course of little value.)

In the cross of VIII×V, the F_1 hybrid is intermediate in shape and size, resembling perhaps the female (VIII) parent more strongly. The F_2 shows a graded series without definite segregation for either shape or size, and including both parental types (fig. 1). In the cross of IV×IX, the F_1 hybrid strongly resembles the male (IX) parent in shape and is intermediate in size, although more nearly like the small parent than the large in this respect. The F_2 again shows a graded series without definite segregation for size (in this case the parental types are not recovered), but there is an apparent monofactorial segregation for shape (fig. 4).

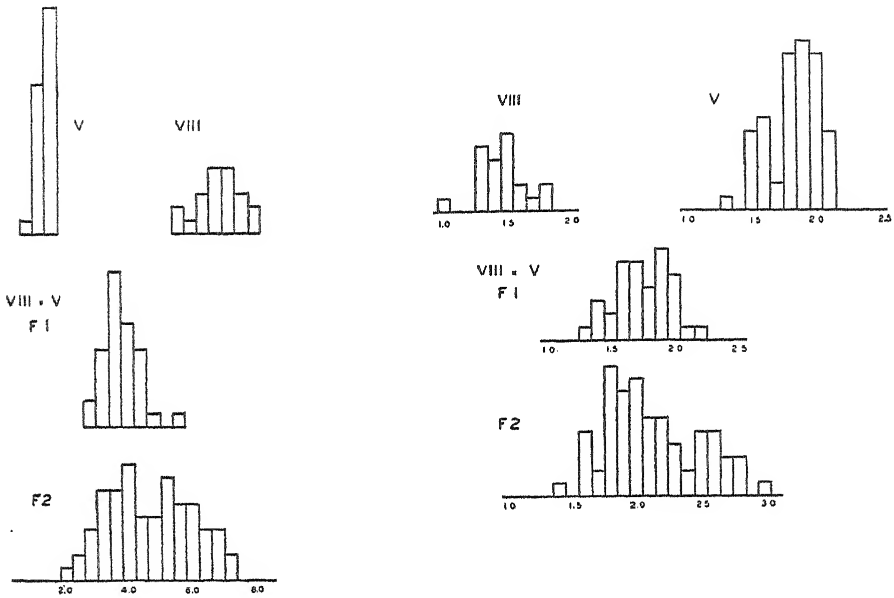

Fig. 2. Dimension distributions in the VIII×V cross. To the left, length in centimeters; to the right, width in centimeters.

An examination of the frequency distributions and the statistics pertaining to them reveals the following facts:

The means of the F_1 are, in almost all cases, intermediate between those of the parents, indicating absence of complete dominance. There is an apparent partial dominance of the male parent in length, shape, and volume in the IV×IX cross. It will be shown later that the dominance in shape is a valid one traceable to the dominant effect of a single gene in development. The dominance in length and volume seems not be very significant, as is indicated by subsequent considerations.

The F_1 means are approximately equal to those of the F_2. The discrepancies which arise (in some cases the F_2 means are larger than those

of either parent) are probably to be explained by the fact that the F_2 plants were grown in the field under more favorable conditions than the others.

In general, variability in the F_2 exceeds that of the parental and F_1 distributions. This increased variability is not especially marked in the volumes of both crosses or in the width of the F_2 of IV×IX. These discrepancies are traceable to the unusually high variability of size for plants grown in pots in the greenhouse. The increased variability of F_2 distribu-

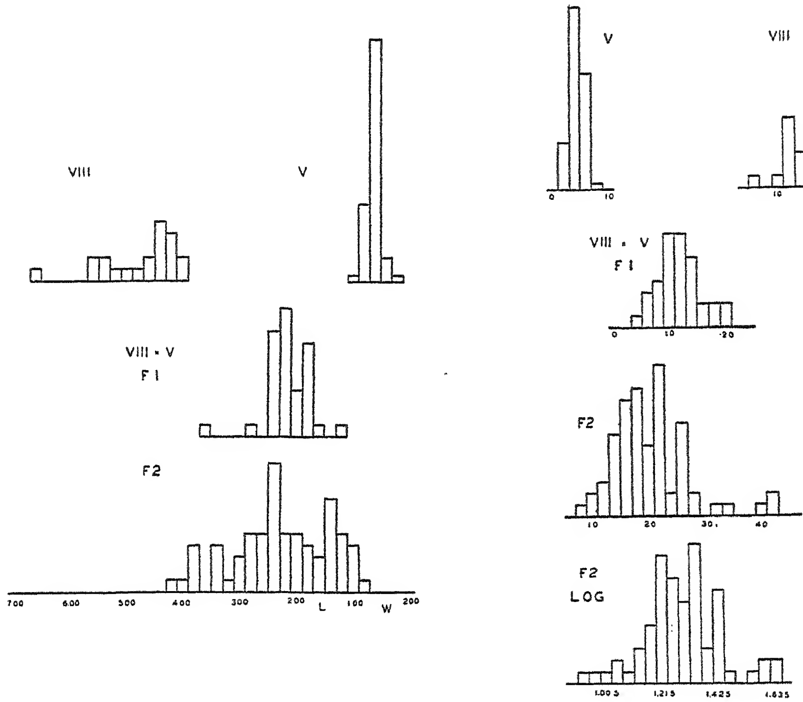

Fig. 3. Shape and size distributions in the VIII×V cross. To the left, shape index; to the right, volume in c.c., and below, the F_2 volumes plotted logarithmically.

tions has generally been interpreted as meaning that a number of genes are assorting and recombining. The question of what the genes directly control, however, has not been at all clarified thus far.

The present evidence supports, for this species, the conclusion of Sinnott (1935) for *Cucurbita* fruits, that genes control shape and total size (volume) rather than particular dimensions. This conclusion was based on the facts that (1) a simple, clearly segregating fruit shape difference is inherited independently of fruit weight (size); (2) there is rarely or never

a significant correlation between fruit weight (size) and fruit shape index in the F_2; (3) shape indices segregate much more sharply than do dimen-

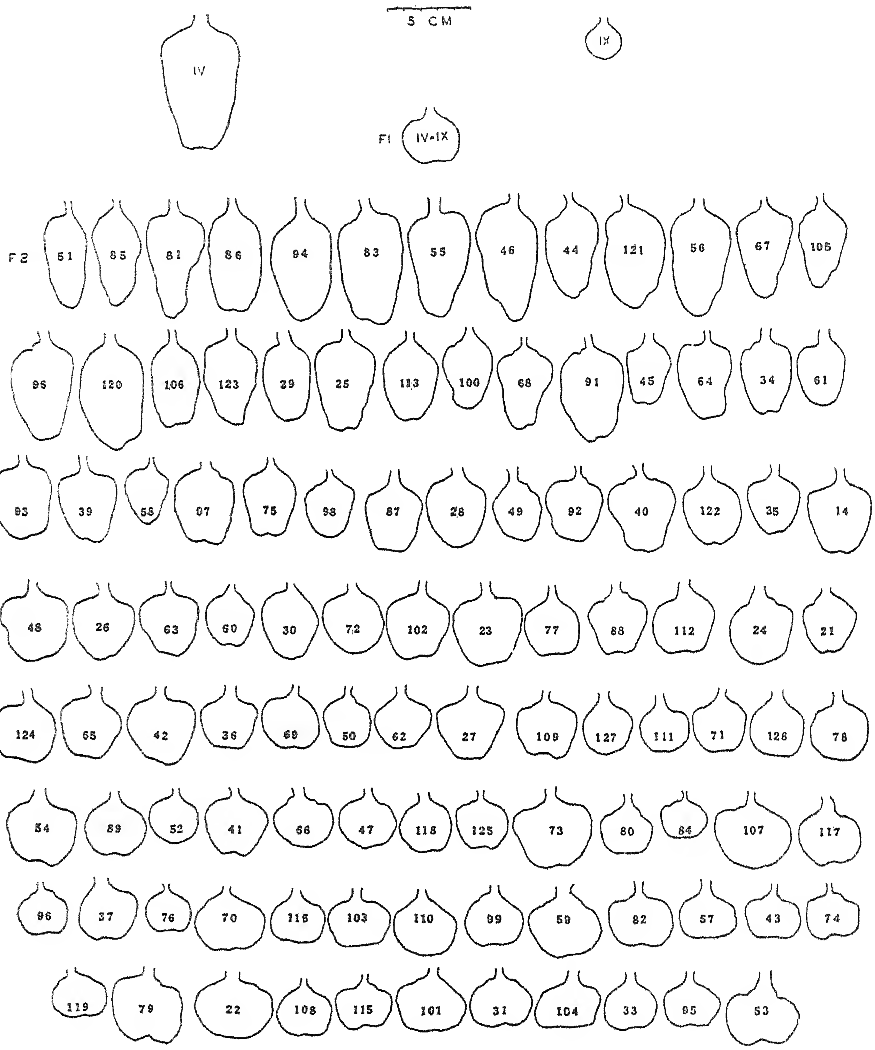

Fig. 4. Trace drawings of typical ripe fruits from the parent plants, IV and IX, the F_1 hybrid between them, IV × IX, and each of the 105 F_2 plants (numbered 21–127), these arranged in a series from the relatively longest to the relatively widest.
Note the monofactorial segregation for shape.

sional traits; (4) there is a positive correlation between fruit length and width in pure lines and F_1 progenies, but a negative correlation between these traits in the resulting F_2 progenies; (5) variability of length is twice

as great as that of width in F_2 generations from crosses between lines which differ in fruit shape, although length and width are essentially equal in their variability in both pure lines and F_1 progenies.

From the present results, it is evident that point 1 is supported by the IV×IX cross but not by the VIII×V cross (figs. 6 and 3). Point 2 is supported by the VIII×V cross (the correlation is only $+.03 \pm .08$), but not by the IV×IX cross, for the correlation here is $+.52 \pm .05$, that is, the larger fruits are in general the more elongate ones. Point 3 is sup-

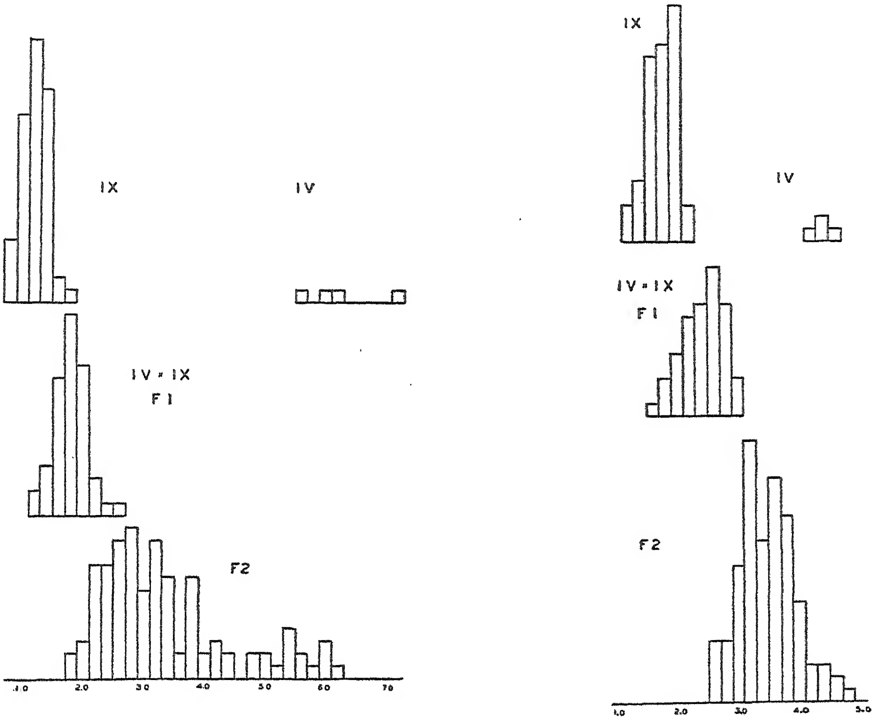

Fig. 5. Dimension distributions in the IV×IX cross. To the left, length in centimeters; to the right, width in centimeters.

ported by the IV×IX cross, but not by the VIII×V cross (see distributions in the figures). Point 4 is supported by both crosses (in the F_2 of IV×IX this correlation is not negative, but is not a significant positive correlation: tables 1 and 2). Point 5 is supported by both crosses (see summaries of statistics).

Thus the present evidence can be interpreted most simply on the basis that genes controlling shape and total size (volume) are operative and that particular dimensions are merely the resultants of the interaction of these.

A genetic analysis of shape, relatively simple in the cross of IV×IX, is very complex in the cross of VIII×V. The positive correlation of shape index with size in the cross of IV×IX suggests a linkage between genes governing size and shape, similar to that reported by Lindstrom (1928) for certain tomato fruits.

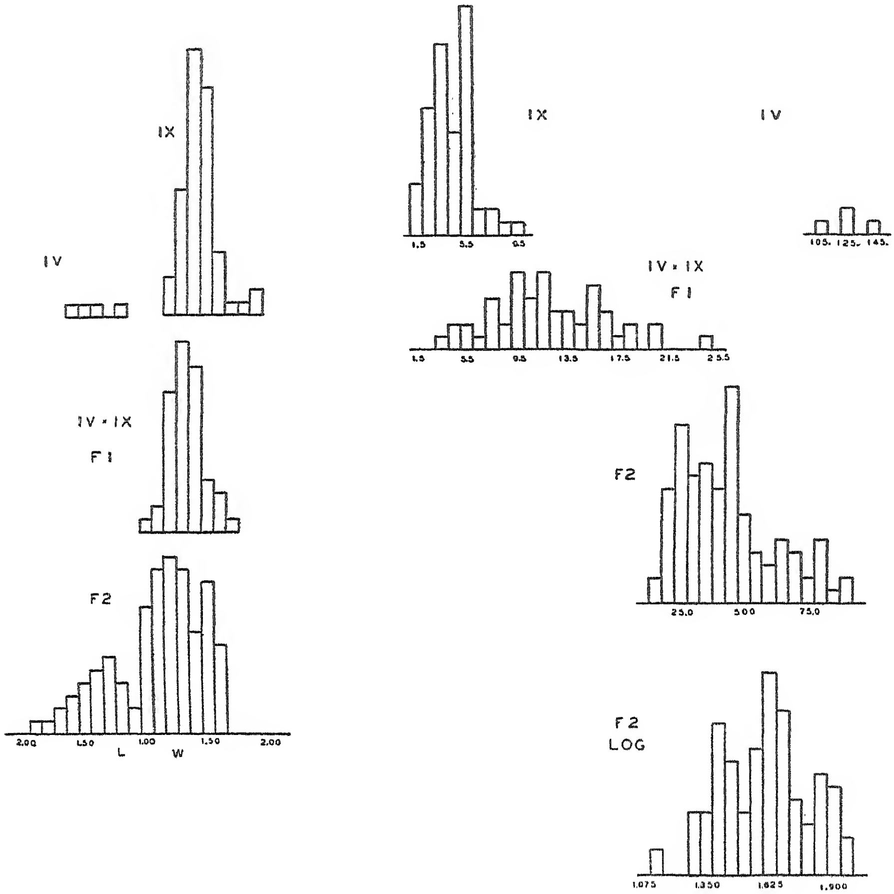

Fig. 6. Shape and size distributions in the IV×IX cross. To the left, shape index; to the right, volume in c.c., and below, the F_2 volumes plotted logarithmically.

With regard to the inheritance of size, the data are not conclusive. One obvious reason for this is the inadequate number of measurements; another, the non-uniformity of environmental conditions; a third, the rather extreme variability of fruit size even under the reasonably well-controlled conditions of the greenhouse. The results are best explained on the multiple-factor hypothesis by assuming a number of genes controlling

by their interaction the final size of the fruit. This number must be fairly small in the VIII×V cross, since the parental types were recovered in an F_2 progeny of only 70 plants. In the IV×IX cross the number is evidently larger.

The question arises as to whether the genes controlling size act additively with partial dominance or geometrically without dominance. The logarithmic treatment of growth data as advanced by Zeleny (1920), Dale (1928) and others has here been applied. The diagnostic feature in this respect is the normalization of skewed arithmetic distributions when plotted logarithmically. Normalization is striking in both crosses, skewness being reduced in the F_2 of VIII×V from +0.45 to +0.01, and in the F_2 of IV×IX from +3.08 to −0.26. Such a result suggests that the several size genes involved in these crosses operate geometrically rather than additively.

In view of the difficulties and complexities arising in this analysis and in the work of earlier investigators, it is apparent that a more detailed analysis is necessary in order to ascertain the genetic mechanism of shape and size determination in these fruits. It is a matter of common observation that in certain fruits (such as the elongate peppers) shape *changes* as growth proceeds. A study of the dimensional changes occurring during fruit development provides an obvious means of simplifying the interpretation of shape and size inheritance in the present material.

DIMENSIONAL CHANGES DURING FRUIT DEVELOPMENT

Huxley (1932) has suggested a method of studying relative growth which has already been successfully applied to the present material (Sinnott and Kaiser, 1934). Here it was shown that if length and width of ovary primordia and fruits in all stages of development, from the earliest ones observable until maturity, were plotted against each other logarithmically, the resulting curve was an essentially straight line for some varieties, while for others it was a sickle-shaped curve. Employing Huxley's formula, $y=bx^k$ where y is length and x is width, we may say that in one type (straight-development) k, the relative growth constant of length to width, remains unchanged during the growth of the fruit; since its value is nearly equal to 1, width is constantly increasing at approximately the same rate as length. In another type of pepper, an elongate one (curved-development), the developmental curve starts out just as in the previous case with the same value for k, but soon after flowering it slopes upward steeply and abruptly, indicating that length has now begun to grow at a considerably faster rate than width. As a result the elongate shape begins to emerge. Shortly before maturity, the value of k falls to 1 or less than 1,

TABLE 3

Type series of developmental fruit measurements in Line VIII, Line V and their hybrid. Asterisk indicates flowering.

VIII		V		VIII×V	
LENGTH CM.	WIDTH CM.	LENGTH CM.	WIDTH CM.	LENGTH CM.	WIDTH CM.
.06	.08	.06	.08	.06	.08
.07	.09	.08	.11	.08	.10
.08	.10	.08	.12	.09	.11
.08	.11	.10	.14	.10	.13
.10	.13	.12	.16	.12	.14
.14	.16	.14	.18	.13	.16
.17	.18	.16	.20	.14	.17
.20	.20	.18	.21	.15	.18
.22	.22	.18	.24	.18	.21
*.24	.24	*.20	.27	.21	.24
.24	.27	.24	.30	*.24	.26
.27	.22	.26	.37	.28	.32
.34	.34	.28	.32	.30	.32
.36	.32	.30	.36	.34	.33
.51	.36	.33	.42	.36	.35
.54	.36	.36	.48	.42	.40
.58	.35	.42	.54	.48	.44
.60	.39	.48	.70	.54	.45
.60	.42	.60	.75	.66	.46
.62	.38	.65	.80	.70	.40
.86	.41	.73	.88	.82	.48
1.10	.45	.85	1.05	.90	.51
1.16	.48	.90	1.20	1.05	.55
1.25	.55	1.00	1.30	1.50	.65
1.50	.58	1.12	1.50	1.50	.75
1.60	.61	1.12	1.85	2.20	1.00
1.70	.63	1.20	1.95	2.37	1.19
1.80	.65	1.27	1.70	3.03	1.16
2.50	.64	1.30	1.82	3.38	1.30
3.20	.73	1.30	2.00	3.61	1.45
3.44	.80	1.39	2.00	4.00	1.45
4.33	.86	1.60	2.30	4.05	1.65
4.90	.98			4.47	1.80
5.20	1.00			4.60	1.86
5.63	1.10				
6.07	1.09				
6.70	1.48				
7.00	1.33				
7.65	1.76				

due probably to the rapid increase in width resulting from the growth of the seeds within the ovary. Thus, in *Capsicum* fruits the stage of development at which shape genes produce their visible effect is a comparatively late one and shape differences are due to differences in the value of k. This determination is quite different from that in *Cucurbita* fruits where

TABLE 4

Type series of developmental fruit measurements in Line IV, Line IX and their hybrid. Asterisk indicates flowering.

IV		IX		IV×IX	
LENGTH CM.	WIDTH CM.	LENGTH CM.	WIDTH CM.	LENGTH CM.	WIDTH CM.
.06	.09	.04	.06	.08	.10
.08	.14	.05	.07	.09	.14
.09	.12	.08	.11	.10	.14
.09	.15	.09	.14	.10	.16
.10	.16	.10	.16	.12	.16
.12	.18	.12	.18	.12	.18
.13	.21	.14	.20	.15	.19
.14	.24	.15	.23	.16	.23
.18	.27	.16	.24	.18	.24
.20	.34	.17	.24	.20	.27
.21	.36	.18	.24	.22	.30
.24	.39	.18	.27	.23	.36
.28	.42	.19	.30	*.24	.30
*.30	.42	*.22	.32	.28	.40
.35	.60	.22	.36	.30	.42
.40	.70	.24	.36	.34	.49
.48	.80	.27	.41	.36	.48
.60	.85	.30	.48	.36	.54
.80	1.00	.32	.48	.40	.60
.85	1.10	.38	.58	.50	.52
.90	1.30	.42	.63	.58	.68
1.10	1.30	.50	.70	.60	.70
1.35	1.35	.55	.80	.60	.80
1.70	1.10	.66	.90	.70	.85
1.90	1.45	.70	1.10	.80	.95
2.00	1.50	.75	1.25	.90	1.15
2.10	1.40	.85	1.18	1.05	1.30
2.50	1.30	.90	1.36	1.15	1.40
2.80	1.85	.90	1.50	1.20	1.50
3.30	1.70	1.10	1.70	1.30	1.80
3.60	1.90	1.20	1.90	1.40	1.40
4.60	2.60	1.36	1.95	1.50	1.90
4.60	3.20	1.50	1.94	1.50	2.20
5.60	4.70	1.59	2.05	1.60	2.20
6.10	4.50	1.85	2.25	1.80	2.40
6.20	4.20			1.80	2.50
7.20	4.50			1.98	2.70
				2.13	2.80
				2.15	3.00
				2.30	3.05
				2.40	3.50

the various shape types are visible in the earliest primordia (due to differences in the value of b in Huxley's formula).

It is of considerable interest to examine the relative growth curves of the fruits involved in the crosses here analyzed.

The VIII×V cross. A type series of developmental measurements is given in table 3. Stages too small to measure with calipers were cut longitudinally and the median sections measured under binoculars with an ocular micrometer. The developmental curves of Line VIII, Line V, their hybrid and a selected series of F_2 plants are shown in figure 7. It will be observed that Line VIII has a sickle-shaped curve, Line V an essentially straight one, and their hybrid a sickle-shaped curve of less steep

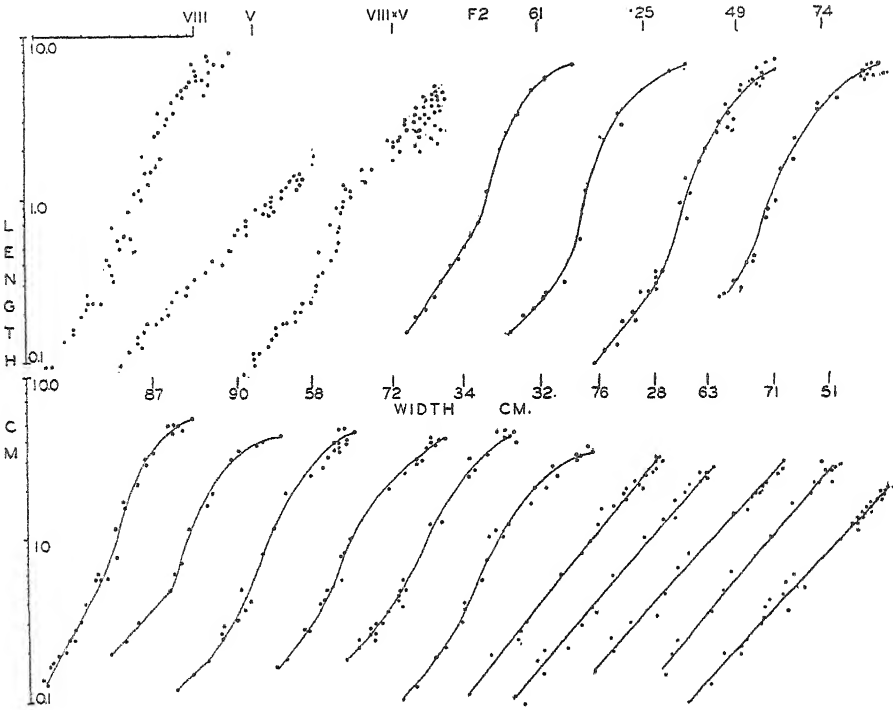

Fig. 7. Developmental curves in the VIII×V cross (above) and the IV×IX cross (opposite page). Curves of the pure lines, the F_1 hybrids and selected series of numbered F_2 plants, arranged in the order of diminishing relative length of mature fruit, are shown. The vertical lines associated with the numbers indicate the position of the 1.0 cm. (width) abscissa line for that curve.

pitch than that of Line VIII. The F_2 progeny segregates clearly into the two parental types of development. Of the forty plants thus analyzed, thirty-one were classified as curved-development types and nine as straight-development ones. In addition, four plants were analyzed but not classified because of insufficiency of measurements or marked irregularities. On the basis of this apparently monohybrid segregation it is postulated that the parental types differed in a single gene (Line VIII

carrying the dominant allelomorph) which governs the relative growth rates of the fruit dimensions in development. It should be emphasized that in the F_2 of this cross, there was *no apparent segregation in mature fruit shape*. It is thus demonstrated that shape genes may be operative in controlling relative dimensional growth rates even though the configurations of the mature fruits do not show Mendelian segregation.

The parent plants have been shown to differ in a gene controlling the

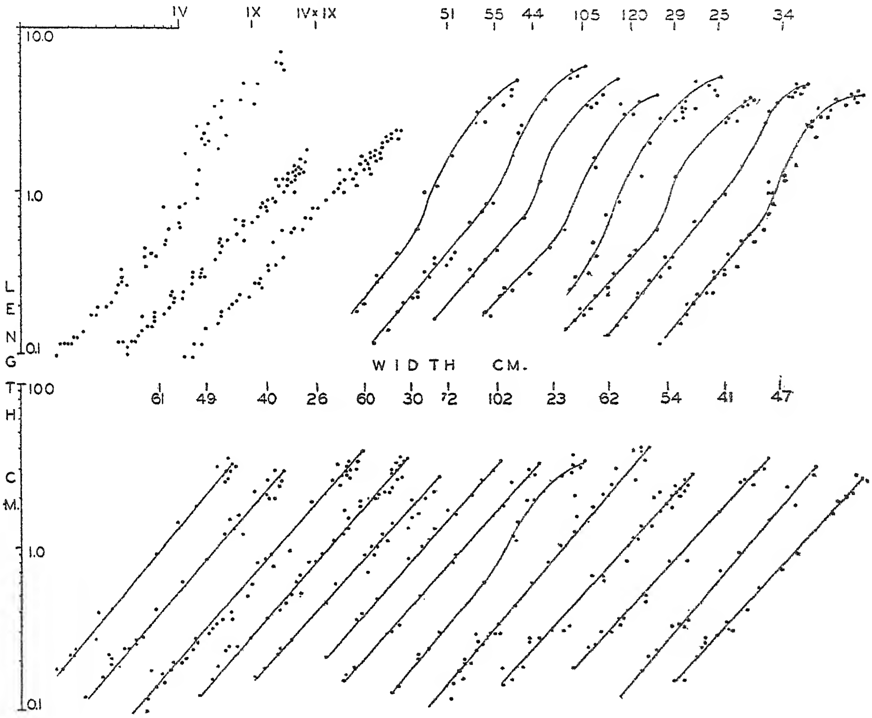

Fig. 7 (continued). See legend under fig. 7 on opposite page.

position of the mature fruit (Kaiser, 1935). On the basis of the forty F_2 plants whose phenotypes with respect to the fruit position character and the developmental curve character are known, it appears that these two genes assort independently.

The IV×IX cross. Type series of developmental measurements for Line IV, Line IX, and their hybrid are given in table 4. The developmental curves of these and a selected series of F_2 plants are shown in figure 7 (page 447). Line IV has a sickle-shaped curve somewhat different in character from that of Line VIII. Line IX has a straight one. The hybrid in this case is straight (but broken?) and the F_2 plants again segregate into

the two main development types. Of the sixty-nine plants analyzed fifteen were classified as curved, forty-eight as straight, and six as doubtful. Here too, then, is an evidently definite monofactorial segregation, but the straight type is dominant over the curved.

Among the F_2 development curves, a number were observed of a wavy, instead of continuous, character (note no. 26). It is difficult, because of an inadequate number of measurements, to say definitely whether this is fortuitous or a true genetic character resulting from recombination. The classification of the F_2 curves into thirty-five straight continuous, thirteen straight wavy, fourteen curved continuous, and one curved wavy suggests that in this cross there may be a secondary shape development gene which influences the character of the developmental curve. It is altogether probable that there are other secondary developmental genes which control the steepness of the curve, its time of departure from the straight line condition, and so on.

Influence of size genes on shape. An examination of the developmental curves presented shows that not only do these curves differ in their general shape, but also in their *length* (extent), or, in other words, the size to which the fruit grows. From evidence previously presented this seems to be determined by genes for size which are quite independent in inheritance from those governing shape.

It seems evident then, that the final configuration of the mature fruit is determined by an interaction between genes which control shape development and those which govern size. This hypothesis explains in a simple manner the results obtained, for very evidently when the relative growth constant for length and width is not 1, the shape index will change markedly with increasing size. This fact, and the knowledge that environmental conditions may influence fruit size to a marked degree, make clear why, in many cases, studies of mature fruit shapes alone result in confused and complicated situations. A knowledge of what takes place during the development of the organ seems to be the key to the solution of the main difficulties encountered in genetic studies of quantitative characters of this sort. These various shape development and size genes operate independently of each other, except where linkage occurs (which seems to be the case in the IV×IX cross), and by their assortment and recombination produce a variety of types in the F_2. These F_2 types show no clear segregation of mature fruit shape indices in the VIII×V cross but fall into two well-defined groups (the parental types) in the IV×IX cross. One might expect that in this latter cross, where a number of size factors are involved, there would also be no clear fruit shape segregation. The apparent linkage between shape and size genes here probably accounts for the results obtained.

It is clear that the genes postulated as a result of the findings of the present investigation must exert their control over fruit shape and size by governing the rates of cell division and cell enlargement and the directions in which these take place. What is the histological and developmental basis for the changes in relative growth rates and size determination which the genes control? Work is at present in progress which may throw light on the relation of cell shape and size to fruit shape and size in this material. A quantity of data obtained from measurements and counts of the ovary wall cells of fruits in various stages of development is at present available, but has not yet been thoroughly analyzed. Several points of interest, however, have already presented themselves.

The pericarp cells particularly studied are the epidermal cells and the cells just inside the inner epidermis, called by Augustin (1907) "Riesenzellen." These interesting cells begin as meristematic cells equal in size and similar in shape to the others but grow at a tremendously accelerated rate, so that in the ripe fruits they attain a size several thousand times their original volume. These giant cells are convenient for study because of their large size, their specific position in the ovary wall, their relatively constant number, and the rapid changes in growth which they undergo. It is clear, from a comparison of these with the epidermal cells that shape and size genes do not influence all the pericarp cells in the same way. The "Riesenzellen" in both curved-development and straight-development fruits are found in the ovary anlage in equal numbers, and of the same shape and size. The developmental curves (for length-width relationship) of these growing cells in both fruit types seem to be the same, following in general the curved-development pattern of elongate fruits (sickle-shaped curve). At maturity they are similar in size and shape in both fruit types, although there is considerable variation throughout the length of the fruit. The outstanding fact, however, is that in the elongate fruits, all the young "Riesenzellen" develop in this way, while in the shortened fruits, only some do so. As a result, although both types have at the start equal numbers of young "Reisenzellen," at maturity the long fruits have a larger number of mature giant cells. In the short fruits, these cells are fewer, having pushed the undeveloped "Riesenzellen" inside. These cells evidently behave differently from those studied in other material by Tenopyr (1918) and Houghtaling (1935).

DISCUSSION AND REVIEW OF PERTINENT LITERATURE

The chief contribution of the present work is its demonstration that, exclusive of the effects of environmental conditions, the ultimate configuration of the fruit of *Capsicum annuum* depends on the interaction between genes governing the relative growth rates of its dimensions and genes

controlling its absolute size. A comparison of the results obtained from the present research with the results of similar work done on other organisms suggests that the theory here proposed in explanation of the genetic determination of shape may be useful in simplifying the complexities which often arise from studies dealing with shapes of mature organs exclusively.

In several cases, specific genes controlling shape have been postulated on the basis of mature organ shape segregations. Leake (1911) obtained in cotton leaves a clear 1:2:1 F_2 segregation for "leaf-factor," a shape character. Sinnott (1927) identified two genes in *Cucurbita*, which by their interaction produce elongate, spherical, and discoid fruits. Lindstrom (1927) found genes in the tomato which determine a number of particular fruit shapes. Hutchinson (1934) described the effects of five multiple allelomorphs in cotton, which control leaf shape. The present case of the IV×IX cross parallels these simple results, but no other results reported for the fruits of *Capsicum annuum* do so. In many species, evidence from studies of mature organ characters indicates that shape as such is not inherited as a simple character. This evidence consists of the intermediate character of the F_1 and/or the continuous nature of the F_2 shape frequencies (Jones, 1911, in *Digitalis* leaves; Groth, 1915, in tomato fruits; Kakizaki, 1930, in eggplants; and Crane and Lawrence, 1933, in apples). The present case of the VIII×V cross parallels these results. But it has been shown for this cross (as well as for the preceding one) that when the fruits are studied developmentally, evidence is obtained of the activity of a single major gene which controls the shape of the organ (at a particular size) by governing the relative growth rates of its dimensions.

Except in the case of dwarf forms, specific single size genes are comparatively rare. Leake (1911) indicated that some may be present in the case of petal size in cotton flowers. Lindstrom (1932) identified several in tomato fruits through linkage studies. Green (1935) located size genes in the mouse on a particular chromosome. Castle (1929), however, failed to find any evidence of linkage of size factors in the rabbit with four known linkage groups. There is considerable disagreement among investigators as to the number and mode of operation of size factors. Rasmusson (1933) is of the opinion that "it is considered more probable that 100–200 genes are usually involved in the segregation of quantitative characters than 2–20." Others believe there are much fewer. Crane and Lawrence (1933) and more recently Lindstrom (1935) hold that size genes operate additively with partial dominance; Dale (1928) and others argue that size genes operate geometrically without dominance. From the present work, it seems clear that in the VIII×V cross a small number of size factors are involved;

in the IV×IX cross the number appears to be larger. The normalization of skewness in F_2 volume distributions when plotted logarithmically suggests that these size genes operate geometrically rather than cumulatively.

A number of investigators hold the position that dimensional characters are inherited (Dale, 1928, and Deshpande, 1933, in pepper fruits; Keeble and Pellew, 1910, and De Haan, 1927, in pea stems; Freeman, 1919, in wheat leaves; Kottur, 1923, in cotton leaves; Sirks, 1929, in broad-bean leaves; Ramiah and Parthasarathi, 1933, in rice grains). According to this idea, shape would not be a definitive hereditary character but would be the resultant of genetically determined dimensions. In almost all of these cases the genetic evidence for dimensional inheritance is at best very complicated and in many instances unconvincing. The present results and those of Sinnott mentioned earlier indicate that apparent segregations of linear dimensions in F_2 progenies are not to be regarded as evidence that genes directly regulating these dimensions exist, but rather that these segregations are the indirect results of interactions between genes controlling dimensional *relationships* during the organ's development, and genes controlling the total amount of growth.

This hypothesis finds support in the conclusions of other investigators working on a variety of materials: "Observations on F_2 bean seeds where the parents differ in size but not in shape indicate that length and breadth are probably not inherited independently of each other" (Emerson, 1910); ". . . what is inherited is (A) a defined rate of relative growth . . . , (B) a defined adult absolute size" (Ford and Huxley, 1927, on *Gammarus* limbs); "The factors determining shape are evidently those which govern growth correlations" (Sinnott and Durham, 1929, on squash fruits); "Particular dimensions are merely resultants of the interaction of these shape and volume factors" (Sinnott, 1931); "He" (Castle on rabbits) "also recognizes that body form is to some extent a function of size . . . that there are growth relations of the sort which Huxley terms heterogonic" (Wright, 1932); "The conclusion is reached that conformation is primarily the result of the interaction of growth factors . . ." (Gregory, 1933, on cattle form); "It follows therefore that size and form show a strong tendency to remain constant or to vary together, not to be modified independently of one another" (Brues, 1934, on insect size).

The importance of studying growth in development as relative growth of parts (or dimensions) rather than as growth of the whole has been emphasized here. This idea has also been stressed not only by Huxley but by D'Arcy Thompson (1917), Pearsall (1927), Robb (1929), and others. A striking demonstration of its value in evolutionary study has also been made by Hersh (1934) in his study of fossil titanotheres. Here it is shown

that changes in size result in profound changes in form when k is not equal to 1. The present paper shows the importance of this kind of treatment in genetic studies. Sinnott (1932) has previously shown that developmental studies are able to clarify complex quantitative segregations.

The developmental genes postulated in the present work apparently operate by controlling growth rates. This is in harmony with Goldschmidt's theory of the genetic determination of characters through the control of rates of reactions. It should be emphasized, however, that these developmental genes govern not merely growth velocities but the *relationships* between these velocities.

SUMMARY

1. The genetic determination of shape and size has been studied in two crosses of *Capsicum annuum* by (1) a statistical analysis of mature fruit dimensions and (2) an analysis of dimensional changes during fruit development.

2. The following facts support the theory that the hereditary control of dimensions is accomplished through the independent genetic determination of shape and of size: (1) In the cross of Line IV×Line IX, mature fruit shape index shows a clear monofactorial segregation in the F_2; in the cross of Line VIII×Line V no such segregation is observed, but the F_2 shows a complex continuous distribution of shape indices; (2) In neither cross are there simple F_2 segregations for length or width of mature fruit; (3) In the cross of Line VIII×Line V there is no significant correlation between shape and size in the F_2; in the cross of Line IV×Line IX this correlation is of the order of plus 0.5 (the longer fruits are in general larger); (4) In both crosses length is positively correlated with width in the pure types and F_1; in the F_2 this correlation is small or negative; (5) Length is almost twice as variable as width in the F_2 of both crosses; in the pure types and the F_1 these variabilities are almost equal.

3. Evidence is presented that in each cross there is a single major gene controlling the *relative* dimensional growth rates of the developing fruit. In some cases the relation between the growth rate in length and that in width is constant, in others it changes as growth proceeds.

4. Size is genetically determined by the interaction of a number of size genes, but is subject to considerable modification by environmental factors. These size genes operate geometrically, not additively.

5. The ultimate configuration of the mature fruit is genetically determined by the interaction between (1) factors governing relative dimensional growth rates and (2) factors governing the size of the fruit. In one of the crosses, these two types of genes are probably linked.

6. Developmental analyses are thus able to simplify complex genetic data obtained from studies of mature organs.

ACKNOWLEDGEMENTS

The writer is grateful to the directors of the Brooklyn Botanic Garden, the New York State Institute of Applied Agriculture and the Marine Biological Laboratory for the use of land during the summers of 1932, 1933, and 1934 respectively. He wishes to acknowledge his indebtedness to Miss Selma Rice for her assistance in the statistical work and to Mr. H. G. Albaum for his help in the preparation of the figures. He is deeply appreciative of the generous help and encouragement given him by Prof. E. W. Sinnott, under whose guidance the work was carried out.

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Origin and development of the female gametophyte, endosperm and embryo in Orobanche uniflora[1]

JOSEPHINE D. CASSERA

(WITH PLATES 25–28)

INTRODUCTION

Orobanche uniflora L. (*Aphyllon uniflorum* T. & G.) is a small parasitic plant growing in moist woods on the roots of goldenrod, clover, aster, etc. It bears a few brownish ovate bracts near the base and sends up one to four erect, slender, one-flowered stalks about three to six inches high. The leaves are reduced to simple, chlorophyll-less scales with an alternate arrangement on the stem. The flowers are solitary, perfect and zygomorphic. The curved tubular five-lobed corolla is purplish or light violet to white with purplish veins. It consists of four or five united sepals and five petals united into a tube. There are four stamens in pairs inserted on the tube of the corolla and often a fifth that is reduced to a staminode. The pistil is bicarpellate with an ovary which is superior, one-celled, and has four parietal placentas. The flower is three-quarters of an inch long and externally is hairy and delicately fragrant. In general the flower structure strongly suggests that of the Scrophulariaceae.

Previous to 1917 relatively little work had been done in the morphology of the Orobanchaceae. In 1917 Scharf surmised that the Orobanchaceae were to be derived from forms which, like the majority of the Scrophulariaceae had a well-developed chalazal and micropylar haustorium. Boeshore (1920) believed that the Orobanchaceae "represents a greatly degraded offspring series or sub-family of parasitic habit that has gradually been derived from Scrophulariaceae in which slow absorption of the ovarian partitions has resulted in a one-celled state from a primitively two-celled." He proves this point by tracing the varied morphological transitional characters between Scrophulariaceae and Orobanchaceae and correlating with this a graded physiological parasitism and degradation. Carter (1928) studied the early embryology of the ovule of *Orobanche minor* and stated that the early development of the megaspore mother cell in *O. minor* was the same as Schertz (1919) described for *Scrophularia marylandica*. Glisic (1929) reported that the embryo-sac development in *O. hederae* and *O. gracilis* were of the normal type occurring in the Angiosperms but the formation of endosperm and haustoria was characteristic of Rhinantheae and Scrophulariaceae—thus confirming Scharf's and Boeshore's work. The

[1] Submitted in partial fulfillment of the requirements for the degree of Master of Science in Rutgers University.

Scrophulariaceae and the Orobanchaceae Glisic concluded agree so thoroughly in their endosperm characters that they could well be united; close relationship between these two families is also seen in seed development.

The purpose of this paper is to present a study of the development of the female gametophyte and endosperm formation in *O. uniflora*, making special reference to any primitiveness or specialization which may have developed as a result of its parasitic habit. During the course of this work, the writer also noted the great resemblance of the Orobanchaceae to the Scrophulariaceae.

The plants studied were collected near Milltown, New Jersey by Dr. M. A. Chrysler in the last week of May and the first week of June, 1933. *O. uniflora* was there found to be growing parasitically on *Solidago rugosa* Mill.

The ovaries of *O. uniflora* showing various stages of development were divested of the sympetalous corolla, leaving the base of it bearing the epipetalous stamens. The larger ovaries were cut transversely and longitudinally to facilitate penetration of the fixative. It was found necessary to exhaust air from the material by suction as it did not sink in the fixative. Various types of fixatives were employed. Carnoy's fluid was found to be too violent in its action and produced great shrinkage even though the material was left in the fluid only fifteen minutes. Material fixed in Carnoy's was useless for cytological study of the early stages of development of the ovule and embryo-sac, but proved successful in the fixation of the mature buds. Chrom-acetic acid and Allen's modification of Bouin's solution "PFA$_3$" gave results which proved to be excellent for detailed study. The buds were embedded in paraffin and serial sections of five microns and seven microns were cut and fastened serially to slides. Heidenhain's iron-alum haematoxylin counterstained with orange G in clove oil was the most suitable stain. No detail was seen without the orange G which served as a valuable background for bringing out the structure and content of the nucleus. Safranin counterstained with crystal violet was also used but details of the nucleus were not clearly seen.

OBSERVATIONS AND DISCUSSION

In *Orobanche uniflora* the microsporangiate structures have reached the mother-cell stage before the megasporangia become visible as projections from the placenta. The differentiation of the megasporangium begins with rapid cell-division in the epidermis and hypodermis which results in the even surface of the placenta becoming a mass of crowded blunt protuberances. In these the megaspore mother cell is first differentiated as an enlarging hypodermal cell rich in cytoplasm and showing a conspicuous

nucleus. The nucellus next appears as an arch of small cells at the tip of the megaspore mother cell and proceeds to surround the entire megaspore by laying down anticlinal walls. At this stage the walls of two or three outer cells of the ovule begin to bulge outward and form the integument, which is single but has a thickness of four to six cells (fig. 1). The epidermis on the side of the integument facing the nucellus then develops into a conspicuous nutritive jacket.

The megaspore mother cell next increases in size. In appearance it is an elongated cell with a large nucleus and nucleolus. In the resting stage the nucleus shows a peripheral reticulum with strands extending towards the nucleolus. On the whole the appearance of the nucleus is that of a hollow body with a non-staining nucleolus (fig. 2).

Formation of the embryo-sac

The megaspore mother cell then elongates and undergoes two consecutive divisions giving rise to a linear tetrad of megaspores (figs. 2, 3, 4). The tetrad condition was observed in every case, contrary to Miss Smith's (1901) report that the mother cell does not divide in *Aphyllon uniflorum*. After a short rest period, the chalazal megaspore, the only one to function, begins to enlarge by digesting and absorbing the other three megaspores, which gradually become smaller (fig. 4) and later disappear. They are recognized in their late stages of degeneration as shrunken dark cells or as shapeless masses on the edge of the functional megaspore (figs. 5, 7).

After a period of growth the nucleus of the functional megaspore divides into two large nuclei (fig. 6). During this division the funiculus and integument grow more rapidly on one side causing the ovule to curve around and the micropyle to lie close to the funiculus. Thus the ovule is of the anatropous type at the time the two-nucleate stage of the embryo-sac is reached. The nuclei then migrate to opposite poles of the embryo-sac and divide simultaneously, forming spindles which lie approximately at right angles to one another (fig. 7). Very few four-nucleated embryo-sacs were observed, and when observed, the resulting four nuclei were of unequal size. A large vacuole occupies the median portion of the sac. The same condition was reported by Miss Carter (1928) for *O. minor*. As the embryo-sac grows it pushes its way through the micropylar end of the nucellus and absorbs the food released by the breaking down of this layer. By the time the eight-nucleated embryo-sac is formed the nucellus has almost disappeared although traces of it are seen as dark masses or streaks along the megaspore wall of the embryo-sac. The absorption of the nucellus by the growing embryo-sac thus causes the nutritive layer (to be described later) to lie against the megaspore wall.

The mature eight-nucleated embryo sac is typical of the Angiosperms, with an egg and two synergids at the micropylar end, two prominent polar nuclei in the center and three antipodals which are in linear arrangement. The last are present at the time of fertilization and persist throughout endosperm and embryo formation (figs. 11, 13, 15, 17, 19), denoting a specialized condition. Persidsky (1926) also reported persistent antipodals for *O. cumana* and *O. ramosa* but Miss Carter (1928) found that in *O. minor* the antipodals disappear long before the time of fertilization so that the mature embryo-sac contains five nuclei instead of the usual eight. The polar nuclei lie near to each other and remain in that position until the pollen tube enters.

Fertilization

Adjacent ovules are not necessarily in the same phase of growth, for fertilized and unfertilized ones are found in the same ovary and even the fertilized ovules are in various stages. Before fertilization the male nuclei are distingushed from the embryo-sac nuclei by their smaller size and deeper stain. The passage of the male nuclei from the pollen tube to the nuclei with which they fuse is very rapid for they are seldom caught in the process. Fertilization and triple fusion occur simultaneously. The male nuclei remain in the resting condition and retain their small size and oval form even while in contact with the female nuclei.

After fertilization the embryo-sac elongates, developing a chalazal and micropylar haustorium, both of which later are filled with endosperm cells. There is variation in the different ovules as to the length which the incipient embryo-sac may attain before division of the primary endosperm nucleus takes place. In some it may grow to considerable length, while in others very little growth takes place until after the first endosperm division.

Endosperm formation

The endosperm development of Angiosperms occurs in two general methods: 1) free-nuclear divisions followed by cell-wall formation and 2) immediate cell-wall formation dividing the embryo-sac into two chambers. The second method is characteristic of Dicotyledons, particularly the saprophytes and parasites; *Cuscuta* (MacPherson, G. E., 1921) being the only parasite studied with the free nuclear type. The cause of the difference in endosperm development is not known but it is probably connected with the nutritive mechanism of the female gametophyte.

Endosperm development in *O. uniflora* is cellular from the beginning. In the first stage the fusion nucleus divides transversely in the middle of the embryo-sac and forms two chambers, a micropylar and a chalazal

endosperm chamber (figs. 10, 11). A rest period follows this division, during which time no cellular divisions occur although the surrounding cells are active. Upon renewal of nuclear activity the micropylar nucleus takes the lead by forming the micropylar haustorium as well as the endosperm proper. After a slight delay the chalazal chamber becomes binucleated and by its elongation functions as the chalazal haustorium. This does not undergo any further divisions. The micropylar development takes place along two divergent lines which will be discussed separately and referred to as type *A* and type *B*. They differ only in the early stages but soon converge and in late endosperm development both types increase in breadth in the same manner.

Type *A* is more common. The nucleus in the micropylar chamber undergoes division to form a longitudinal wall which gives rise to two elongated cells. Thus, at the end of the second stage there are present three endosperm cells (fig. 12). The nuclei of the micropylar cells become very prominent and elongate in the direction of the resting zygote (fig. 12). As a result of their division, cross-walls are formed, separating the micropylar haustorium from the endosperm proper (fig. 13). It is obvious that the micropylar haustorium arises from the endosperm and is not a modified synergid as was believed by Schlotterbeck. The third stage terminates with five endosperm cells, one of which is binucleate, acting as a chalazal haustorium. The nuclei of the elongated cells give rise to endosperm proper by their simultaneous divisions so that four (fig. 17) and later eight endosperm cells (fig. 18) result. Further development continues by the formation of transverse walls. As a consequence the fourth stage of development ends with two definite rows of cells. Another rest period now ensues, the only sign of activity being a swelling of the nutritive jacket which surrounds the gametophyte.

Although type *A* is more common, type *B* is also frequent and is usually present in the same ovary. The two types may be found side by side but are sharply distinguished from one another in the early stages of development. After the primary endosperm cell has laid down the transverse wall dividing the embryo-sac into chalazal and micropylar chambers (fig. 11), the micropylar chamber elongates somewhat and divides transversely. Consequently the gametophyte consists of a chalazal haustorial cell and two endosperm cells (fig. 14). The nuclear division of the chalazal haustorium next takes place as in type *A*. In stage three transverse walls are laid down rapidly throughout the entire length of the elongated micropylar chamber. Longitudinal walls next make their appearance and by the end of the fourth stage the two rowed condition of endosperm development is reached as in type *A*.

The later stages of endosperm formation for both types are the same, in which cell walls are formed longitudinally, transversely or obliquely, resulting in a mass of endosperm tissue. As the endosperm development proceeds, enzymatic processes set in and the nutritive jacket cells, along with several layers of cells just without, are absorbed and the material is used by the developing endosperm. The young endosperm occupies only the space outlined by the mature embryo-sac and four to five layers of cells are evident in the surrounding tissues. It is thus obvious that the endosperm tissue is being increased at the expense of the surrounding layers of cells. The later endosperm cells also press sharply into the antipodal end of the sac and the tissue bordering this region as well as the chalazal haustorium soon disintegrate and become compressed into a thin layer. As a result the antipodals come to lie in a tubular sac with the antipodals also in a degenerating state (fig. 19).

Glisic (1929) describes endosperm formation of type *A* for *O. hederae* and *O. gracilis*. He is of the opinion that this is the only type of endosperm development and doubts the results of the earlier investigators, especially Koch, Worsdell and Bernard. These workers report that the first two endosperm divisions result in cross walls that divide the embryo-sac into cells lying in definite tiers, one above the other (type *B*). Glisic then attempts to point out their error by stating that the longitudinal wall is very thin and often lies in the plane of section so is not frequently seen. According to the writer's results for *O. uniflora*, the earlier workers as well as Glisic are probably correct, for the type of development in the different species may differ, since both types occur in *O. uniflora*.

The cells of the two types of endosperm development differ, so it is not possible to mistake those of one type for the other. Two elongated cells result from the second division of endosperm development in type *A*. These cells always have nuclei which are very conspicuous and elongated. On the other hand, the second division in type *B* gives rise to two cells which are definitely box-like or rectangular in shape and contain large round nuclei. Consequently, Glisic is in error when he makes the statement that type *B* is really type *A* in which the longitudinal wall is not visible.

Haustoria

As previously mentioned, early in the development of the endosperm the chalazal chamber of the first endosperm division becomes binucleated and elongates to form the chalazal haustorium. Digestion of the nutritive cells at the antipodal end of the ovule occurs very early by the enzymatic action of the chalazal haustorium. As a result most of the antipodal walls

are broken down, leaving a loose mass of nuclei adjoining the haustorium. This organ represents a stunted haustorium which, contrary to the condition found in the Scrophulariaceae and other Sympetalae, never becomes prominent nor as highly developed as the micropylar haustorium.

The micropylar haustorium is cut off from the endosperm proper at the third division of the micropylar chamber nuclei (fig. 13). The first haustorial cells are seen as two conspicuous bulging cells with very prominent nuclei and dense cytoplasm. These two cells soon elongate and divide (figs. 17, 18) rapidly to form a long haustorium which stains deeply due to its abundant food content. Glisic (1929) reports that Koch was the first to recognize the different portions in the micropylar haustorium. The extreme part of the haustorium, which is the most striking and active, he designates the "fertile" part and the other cells making up the haustorium as the "sterile" portion. This consists of several layers (six to seven) arranged in two longitudinal rows of small plate-like cells. Toward the base this sterile portion broadens and is transformed into regular endosperm tissue.

The haustoria are prominent during the early endosperm development but become less conspicuous and show signs of degeneration; by the time the embryo is completely formed they have disappeared entirely. The chalazal haustorium is the first to degenerate and it gradually flattens until it is observed as a dark cap at the antipodal end of the endosperm (fig. 19). The cause of the degeneration is probably the pressure exerted by the aggressive endosperm tissue, although Persidsky (1929) is of the opinion that the nuclei mass together in the chalazal haustorium and by their impetus cause the rapid degeneration of the haustorium. Subsequently the cavities formed by the haustorial deterioration become narrow and no trace of them is seen in the mature seed.

The extent of the development of the haustoria appears to be related to the thickness of the integument, which in these forms is a source of nutritive supply as well as a protective mechanism. These absorbing organs have been studied particularly in the Labiatae, in certain of the Compositae and numerous Scrophulariaceae (Coulter and Chamberlain, 1903).

Nutritive Jacket

As previously mentioned (p. 457), the nutritive jacket originates from the integumental cells immediately adjacent to the nucellus. The differentiation of these cells occurs prior to reduction division in the megaspore mother cell. After fertilization the nutritive jacket which consists of one layer of cells, divides rapidly to keep pace with the growing gametophyte

(fig. 10). During early endosperm development the cells of the nutritive jacket divide mitotically so that they become binucleated (figs. 12, 13, 15, 16, 17, 18). These nutritive cells grow remarkably large and soon become vacuolated with the two nuclei lying tightly against the megaspore wall. This condition is especially conspicuous in the late endosperm formation when the nutritive jacket is resorbed and replaced by endosperm tissue.

This nutritive jacket is remarkably similar to the tapetal layer in the anther and probably serves the same function. The mitoses occurring in the jacket are all normal and regular and do not show the aberrations often seen in the tapetum. The tapetal cells are more richly supplied with food and their density probably interferes with the extension of the spindle so that abnormal mitoses occur. A similar nutritive jacket has been found to be conspicuous in *Helosis*, *Sium*, many Scrophulariaceae, *Campanula*, Stylidaceae, certain Compositae, *Lobelia*, Primulaceae (except *Leptosiphon*), *Linum*, *Forsythia*, *Amsonia*, *Menyanthes*, Polemoniaceae, *Myoporum*, *Globularia*, *Scaevola*, *Calendula*, etc. (Coulter and Chamberlain, 1903).

Embryo

During all the activity taking place in the formation of endosperm, the zygote has been in a resting condition (fig. 20). The first sign of embryo development is an elongation of the zygote (fig. 21). Nuclear division then occurs dividing the zygote into two cells, an anterior bulbous cell which is the embryo proper and the elongated suspensor (fig. 23). In no instance has the suspensor been found to consist of a series of cells. It is always unicellular and soon resorbed by the embryo (figs. 24, 25). The embryo follows the normal sequence in development but remains very rudimentary and minute.

SUMMARY

1. In *Orobanche uniflora* L. the microsporangiate structures have reached the mother cell stage before the megasporangia become visible as projections from the placenta.

2. The megaspore mother cell is differentiated as an enlarging hypodermal cell.

3. The nucellus consists of a single layer of cells.

4. The integument is single but consists of many layers of cells.

5. The integumental cells immediately adjacent to the nucellus differentiate to form the nutritive jacket. This differentiation occurs at the

time the megaspore mother cell is about to undergo reduction division.

6. The ovules are of the anatropous type.

7. The megaspore mother cell undergoes two consecutive divisions giving rise to a linear tetrad of megaspores; the chalazal one gives rise to the embryo-sac, while the other three degenerate.

8. The mature eight-nucleated embryo-sac is of the typical angiospermous type with an egg and two synergids at the micropylar end, two prominent polar nuclei in the center and three antipodals which have a linear arrangement; they are present at the time of fertilization and persist throughout endosperm development.

9. Fertilization and triple fusion occur simultaneously.

10. Endosperm development is cellular from the beginning. The fusion nucleus divides transversely and two chambers are formed, a micropylar and a chalazal one. The development of the micropylar part takes place along two divergent lines. These differ only in the early stages but soon converge and in late endosperm development both types increase in breadth in the same manner. The chalazal chamber becomes binucleated, elongates and functions as a chalazal haustorium in both types.

11. A well-developed micropylar haustorium and a stunted chalazal haustorium are active during endosperm development but degenerate and entirely disappear during late embryo development.

12. A very conspicuous and highly specialized nutritive jacket surrounds the gametophyte; the endosperm tissue ultimately resorbs this layer.

13. The embryo follows the normal sequence in development but remains very minute and rudimentary. The suspensor is always unicellular and is soon resorbed by the embryo.

14. The nutritive mechanism in *O. uniflora* is very complicated and efficient, nutritive substances being derived from the nucellus by the growing embryo-sac; from the nutritive jacket by the embryo and newly formed endosperm cells; and from the integument by the encroachment of the haustoria.

The writer wishes to express her appreciation to Dr. M. A. Chrysler, under whose direction this work was carried out, for valuable suggestions, helpful advice and criticism.

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Explanation of Plates

Drawings were made with an Abbé camera lucida at table level. Zeiss 5×, 10× and 15×oculars and a Spencer 1.8 mm. oil immersion objective were used. Abbreviations used in the plates are: CEC, chalazal endosperm chamber; CH, chalazal haustorium; E, endosperm; EM, embryo; LA, linear antipodals; MEC, micropylar endosperm chamber; MH, micropylar haustorium; NJ, nutritive jacket; S, suspensor, Z, zygote.

Plate 25

All drawings are magnified ×1156.

Fig. 1. Young ovule showing the megaspore mother cell, single layer of nucellus and the integument still in its formative stage.

Fig. 2. Megaspore mother cell.

Fig. 3. Two-nucleated megaspore mother cell.

Fig. 4. Linear tetrad of megaspores with the chalazal one enlarging at the expense of the other three.

Fig. 5. Functional megaspore; the other three in a degenerated condition.

Fig. 6. Two-nucleated embryo-sac with the three outermost megaspores still present.

Fig. 7. Two-nucleated embryo-sac in process of division.

Fig. 8. Four-nucleated embryo-sac.

Fig. 9. Mature embryo-sac.

Plate 26

All drawings are magnified ×528.

Fig. 10. First division (transverse) of primary endosperm nucleus. Nutritive jacket surrounds the megaspore wall.

Fig. 11. Micropylar and chalazal endosperm chambers. Antipodals in linear arrangement at antipodal end of embryo-sac. Zygote in resting condition.

Fig. 12. Second division (longitudinal as in type *A*) of endosperm nucleus resulting in three endosperm cells.

Fig. 13. Third division (transverse as in type *A*) in endosperm development resulting in five endosperm cells. Nutritive jacket conspicuous and binucleated. Antipodals and zygote also seen.

Fig. 14. Second division (transverse as in type *B*) occurs in micropylar chamber, resulting in three endosperm cells, one of which constitutes the chalazal haustorium.

Fig. 15. Simultaneous divisions (transverse as in type *B*) occurring in micropylar chamber. Chalazal haustorium is binucleated.

Plate 27

All drawings are magnified ×528.

Fig. 16. Endosperm formation accomplished by transverse walls (type *B*). Binucleated condition of nutritive jacket clearly seen.

Fig. 17. Nuclei in act of division to give four-celled endosperm stage of type *A*. Zygote and antipodals also present.

Fig. 18. Nuclear divisions which will result in eight-celled endosperm stage of type *A*.

Fig. 19. Complete endosperm formation. Chalazal haustorium almost gone; micropylar haustorium also in degenerating condition. Embryo is embedded in endosperm tissue. No trace of nutritive jacket seen.

Plate 28

All drawings are magnified ×750.

Fig. 20. Resting zygote.

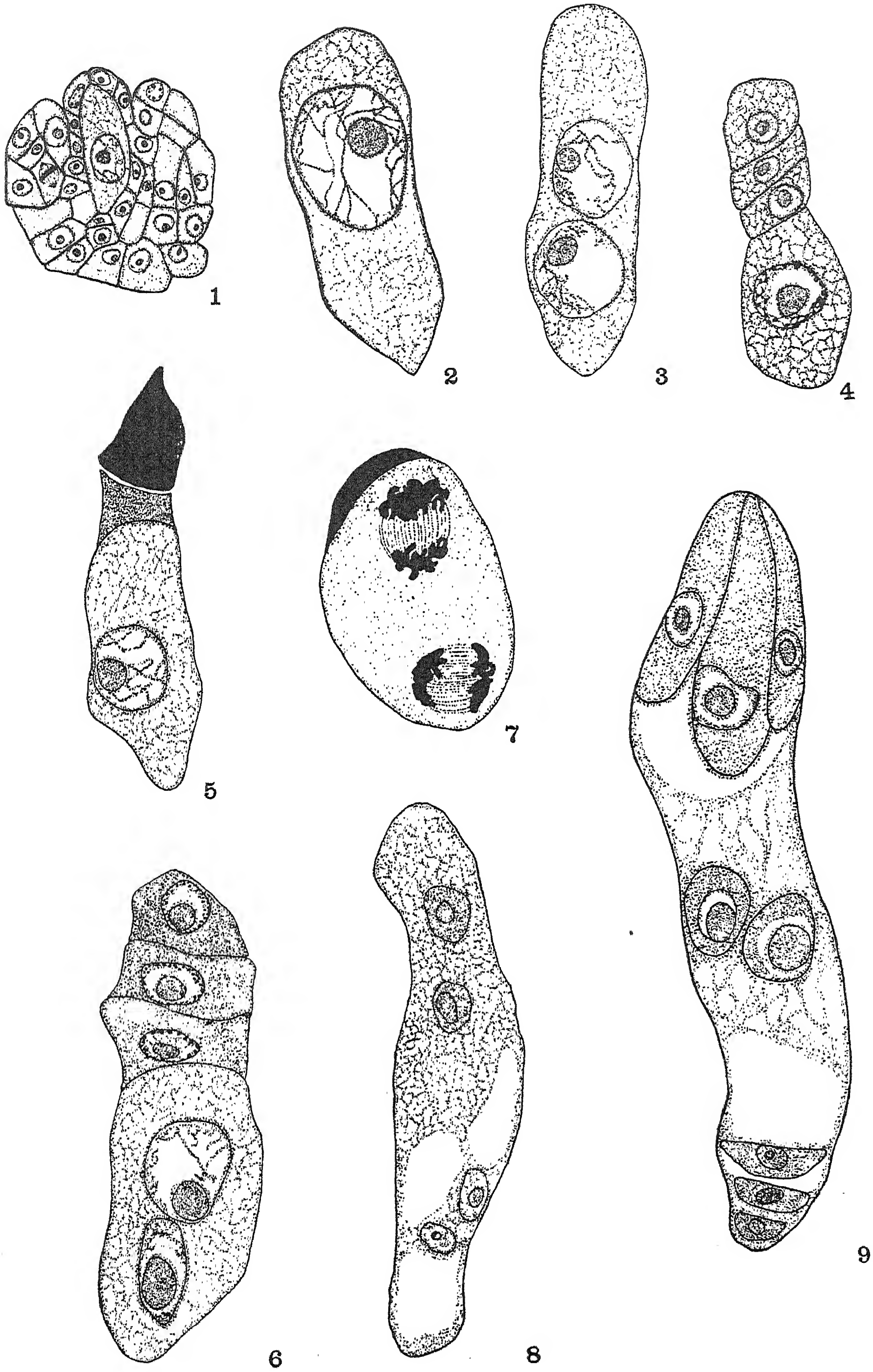
Fig. 21. Zygote in act of elongation prior to first division.

Fig. 2. Spindle of first zygote division.

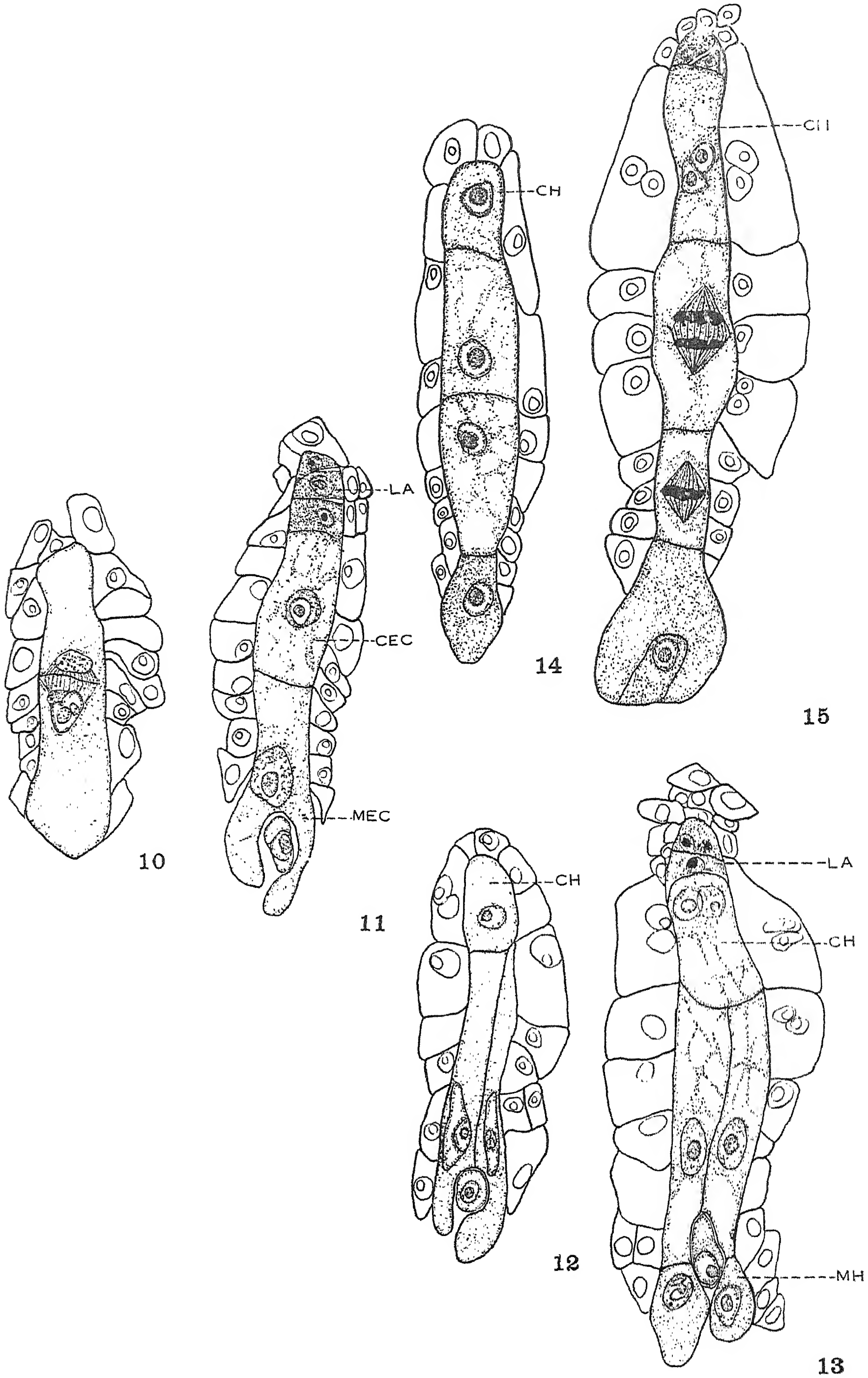
Fig. 23. First zygote division (transverse) resulting in embryo and elongated suspensor.

Fig. 24. Longitudinal division of embryo and resorption of suspensor by embryo.

Fig. 25. Young embryo.



CASSERA: OROBANCHE



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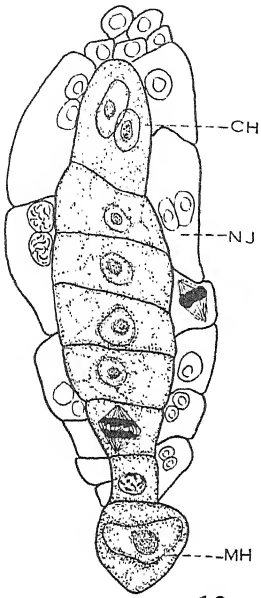

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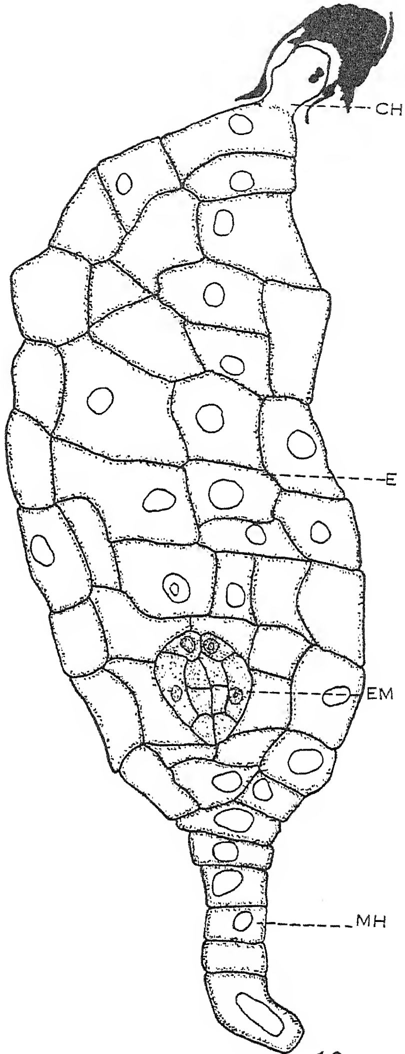

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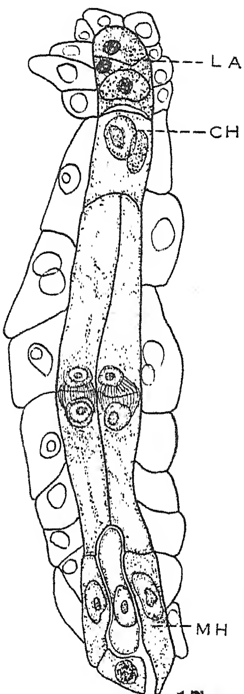

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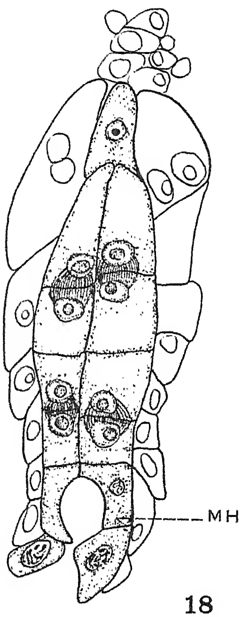

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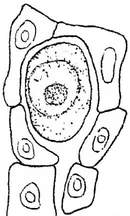

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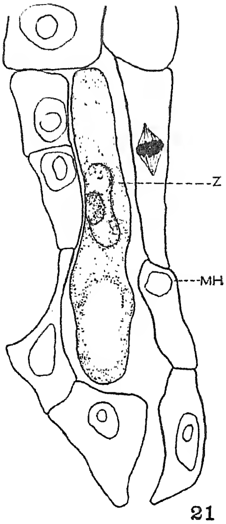

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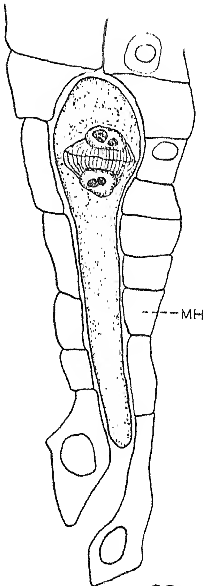

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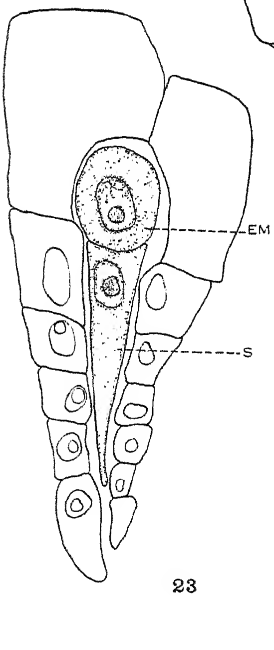

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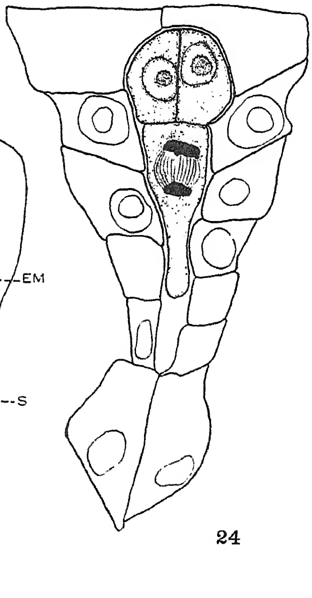

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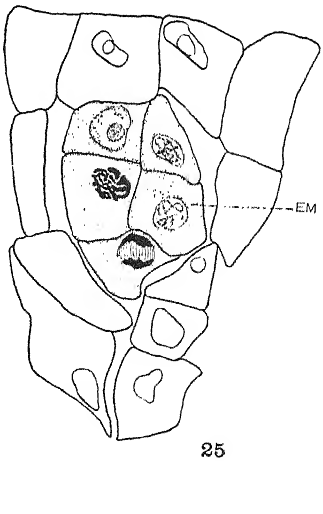

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CASSERA: OROBANCHE

The floral anatomy and probable affinities of the genus Grisebachiella

Robert E. Woodson, Jr.

(with two text-figures)

The vast plateau of Patagonia, extending from the Atlantic coastal plain westward to the Andes, and roughly comprising the Argentine territories of La Pampa, Neuquen, Rio Negro, Chubut, and Santa Cruz, is one of the botanical enigmas of South America. Predominantly somewhat barren and with but relatively scant and monotonous vegetation, the gradually uplifting terrain is traversed by several streams of considerable size draining from the foothills of the western mountains. Small seasonal lakes are found almost throughout the region; arid hills disrupt the nearly flat or rolling topography at monotonous intervals. This country is Argentina's "wild west"; and like most grazing countries, it is of little attraction to the botanical collector to whom it is consequently little known. Among the foothills of the Andes to the west, however, Patagonia is of an entirely different aspect. The boundary between Chile and Argentina is strewed with innumerable lakes of great charm and a luxuriant vegetation of much interest exists.

Our knowledge of the plants of Patagonia is largely dependent upon the collections of P. G. Lorentz and G. Niederlein during the past century. During the course of a collecting expedition to the upper valley of the Rio Negro in June 1879, the latter collected at two localities ("en los declives de las barrancas en las orillas del Rio Neuquen; entre el Rio Curruleubu y el Rio Colorado.") a peculiar flowering plant which was subsequently described by Dr. Lorentz (1880) as a new genus and species which he named *Grisebachiella Hieronymi*, the specific epithet commemorating Dr. G. Hieronymus in whose company the author had spent some time in the botanical exploration of Argentina.

Grisebachiella Hieronymi is a low undershrub said by the collector of the type specimen to attain a height of two to three decimeters, the stems woody, 0.5–0.75 cm. in diameter at the base, the surface with a smooth, pale yellow periderm bearing relatively distant, horizontal lenticels when fully mature. The phyllotaxy is decussate and the branches are opposite. The leaves are relatively inconspicuous, 1.0–1.5 cm. long, shortly petiolate, and ovate, the apex acute to obtuse, minutely mucronulate, the base rounded to truncate. The texture of the leaves is subcoriaceous, the color pale green, somewhat glaucous, and the surface glabrous; the margin is entire. No glands or other special emergences are borne upon the midrib or

petiole. The inflorescence is lateral and uniflorous. About midway upon the stalk of the flower a poorly developed protuberance is found, suggestive of a vestigial floral member. This "stalk" varies from 0.15 to 0.2 cm. in length and is strongly reflexed at maturity. The five-parted calyx is finely papillate without, like the axis of the inflorescence, and the lobes are broadly oblong, averaging about 0.2 cm. in length. At the base of the calyx within are found very inconspicuous groups of glandular emergences or "squamellae" alternating with the lobes. The corolla is rotate and five-parted, the lobes are obliquely oblong, about 0.15 cm. long, and the extremely short tube somewhat less than 0.05 cm. in diameter at the base. Like the calyx, the corolla is minutely papillate without. The very minute anthers are attached to the base of the corolla-tube and are approximately 0.05 cm. long. The pistil consists of two carpels united at their apices by a short, common style surmounted by a capitate, obscurely bilobed stigma about equal to the bulk of the ovary. The anthers are closely connate and appressed to the stigma.

Although none of the available specimens of Niederlein's original collections show any trace of fruit or fruiting pedicels, Lorentz (1880) referred very vaguely to such in his description ("Fructus fragmentum solum modo obtinuimus;" "fructus completus et semina deficiunt."), and in a plate published the year following (1881) a figure is introduced purporting to illustrate the fragmentary fruit, which is unrecognizable as such, evidently consisting of a loose and detached mass of tissue from a larger object. The very dubious status of our information concerning the fruit of the genus will become increasingly evident from structural details of the gynoecium to follow.

Dissection rendered difficult by the small size, and interpretation uncertain by the scantiness of the material available for his study, Lorentz assigned the new monotypic genus to the family Apocynaceae, subfamily Echitoideae where it has since remained. In 1895 Dr. K. Schumann (1895) reviewed the Apocynaceae for Engler & Prantl's "Die natürlichen Pflanzenfamilien," but was so baffled by *Grisebachiella* that he merely stated that he had been unable to investigate it ("Die Gattung *Grisebachiella* Lorentz . . . habe ich nicht untersuchen können."), a peculiar situation, since the Berlin herbarium is the repository of the type specimen.

In 1897 the second, and apparently the most recent, collection of the species was made by P. Dusen: "ad Rio Limay, prope Lago Nahuelhuapi," one of the picturesque lakes of the Chilean-Argentinan border. Unfortunately fruit was again unavailable for this collection, which was made nearly a month later than that of Niederlein.

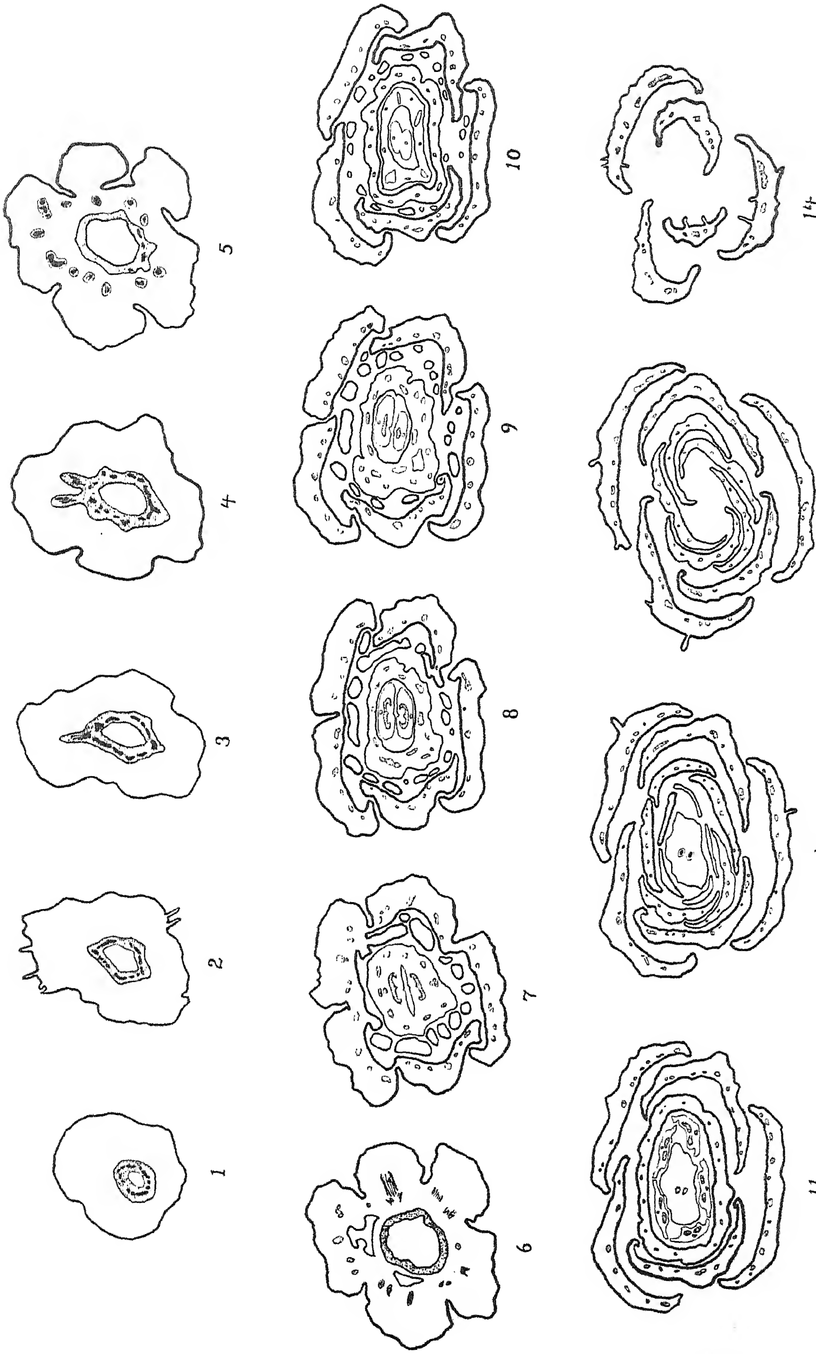

Fig. 1. Transverse sections of the pedicel and flower of *Grisebachiella Hieronymi* Lorentz. Xylem shaded, phloem stippled, anther and ovary cavities cross-hatched.

During the course of a survey of the American genera of the subfamily Echitoideae of Apocynaceae the present writer was faced with the necessity of a greater understanding of the morphology of the obscure *Grisebachiella Hieronymi*, and made a special effort to obtain material for study. No specimens were found in the herbaria of the United States, and upon visiting and inspecting most of the larger collections of Europe only the two specimens of Niederlein and that of Dusen were found in the botanical museum at Berlin-Dahlem. Inquiry of the Museo Argentino de Ciencias Naturales brought the report that the genus is unrepresented in the herbarium of that institution.

The three herbarium specimens available were graciously lent upon request by Dr. L. Diels, director of the Botanischer Garten und Museum, Berlin-Dahlem, for convenient morphological study at the Missouri Botanical Garden. From each of the specimens a single well-formed floral bud was removed. Care was taken to select the buds at the same relative stage of development, e.g. at about anthesis. They were then soaked in a stender dish of water placed in a paraffin oven at about 50°C. for a period of four days. Various methods have been recommended by the relatively few morphologists who have used herbarium specimens for the study of floral anatomy, including such softening agents as dilute solutions of caustic potash and ammonia water. These had been tried previously at various times with rather dubious success by this writer, who consequently decided to try the substitution of the proprietary reagent "Diaphanol" after the soaking in warm water. After treatment with that reagent for three days, the material was washed in 70% ethyl alcohol and passed through the usual series of alcohol and xylol to paraffin. The material sectioned well at 10μ and the serial, transverse sections were stained in crystal violet and erythrosin.

The stele of the pedicel of *Grisebachiella Hieronymi* is bicollateral, as in all known Apocynaceae and Asclepiadaceae, and consists of a number of protoxylem strands embedded in a cylinder of protophloem parenchyma (fig. 1, diag. 1). As the stele gradually approaches the receptacle it increases somewhat in volume and diameter, assuming a roughly pentagonal outline in transverse section (fig. 1, diag. 2). The central pith has increased in volume, and it is also seen that the amount of protoxylem strands have noticeably multiplied. The increase of xylem is found to continue in the two succeeding sections illustrated, during the first of which each of the five angles of the pentagonal stele prepare to supply the calyx-lobes with a single trace (fig. 1, diag. 3). In the second section (fig. 1, diag. 4), the five prominent angles gradually become somewhat greater in number, evidently approximating the traces of all ten perianth members.

In figure 1, diag. 5, the five traces have been freed to the calyx-lobes, the bases of which are becoming cleft from the non-vascular tissues of the receptacle. These traces give rise to two or four laterals shortly after leaving the stele. It will be noticed in diagrams 5–6 of figure 1 that the withdrawal of the calyx traces removes all xylem from the receptacular stele which remains. Whether the state of the stele should now be described as provascular, or as composed entirely of protophloem parenchyma is somewhat problematical. In diagram 6 it is seen that the stele assumes a roughly circular outline at about the time that the calyx-tube becomes cleft from the receptacle proper. At even the earliest stages of this cleaving, however, the origin of the squamellae is found to be marginal with respect to the concrescent margins of the calyx-lobes.

Figure 1, diag. 7 discloses the further splitting of lateral veins in the calyx. In these, however, the last trace of xylem has disappeared. The calycine squamellae have increased in number, and are assuming a circular position about the base of the corolla-tube. The corolla-tube is found to be adnate to the base of the bicarpellary ovary, the two cavities and inconspicuous axile placentae of which are seen separated by a conspicuous cavity. Ten delignified bundles occupying the coralline tissue are interpreted as the bundles of the five corolla-lobes and the five epipetalous stamens, although there appears little with which to actually distinguish them, save by their positions relative to the calyx-lobes. From two bundles at diametrically opposite sides of the circle of bundles, two smaller, delignified bundles are freed, which are immediately recognizable as the median traces of the two carpels. It is discovered that a curious situation of adnation is presented here, in which the median trace of one carpel (the upper in fig. 1, diag. 7) is adnate to a staminal trace, while that of the other is adnate to a coralline trace.

In figure 1, diag. 8, the carpels have become freed from the corolla-tube. The median traces have not formed laterals, however, and it is consequently not surprising to find that no ovules have been formed upon the marginal placentae. The corolla-tube is becoming roughly pentagonal in this section, the coralline traces migrating to the angles, and there giving rise to two lateral veins each. Diagram 9 of the same figure shows two cavities formed within the thickened angles of the corolla-tube. It is by means of the continued growth of five such cavities that the staminal filaments are finally freed from the corolla-tube. It should be noticed in the succeeding diagram that although the union is brief, a staminal column must doubtless be interpreted. In this diagram also, the first indications of the segmentation of the individual, staminal filaments is apparent as a series of radial furrows. In figure 1, diag. 11 a section is illustrated through

the anthers and stigma. The anthers are found to contain but two rather small cavities. Within the cavities were found a number of small pollen grains without an exine. The fact of their maturity, however, was indicated by their maintenance in gradually disintegrating tetrad formation. The cells of the herbarium material had been sufficiently preserved in spite of desiccation to show contents, and the general tissue systems were conspicuous. It is of great importance to emphasize at this point that the remains of the tapetal layer, as a parietal layer of disorganizing, *isolated* cells was obvious. The median traces of the carpels have continued unbroken to the stigma, while the dorsal and lateral traces of the corolla-tube have broken up into a larger number of equal veins.

Diagram 12 of figure 1 illustrates a section through the free tips of calyx- and corolla-lobes and anthers. A surprising phenomenon, however, is seen in the increased size of the carpellary traces of the stigma, which have suddenly acquired several strands of protoxylem for either. It is difficult to assign a causal function for this sudden return of lignification. No evidence of glandular cells could be found upon the stigmata. Diagrams 13–14 of figure 1 merely complete the anatomical representation of the flower.

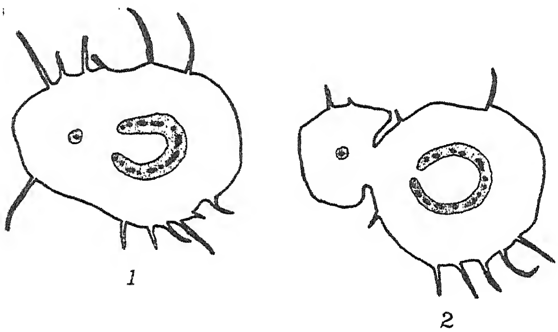

Fig. 2. Transverse sections in the region of the bracteate node, inflorescence of *Grisebachiella Hieronymi* Lorentz. Xylem shaded, phloem stippled. Explanation in the text.

Figure 2 represents the anatomy of the peculiar protuberance previously mentioned as occurring midway upon the "stalk" of the solitary, lateral inflorescence. The "protuberance" is found to be a minute appendage provided by a single leaf-trace which is lignified. Upon the departure of this tiny bract, two glandular, marginal emergences are formed at the base, which are evidently the homologues of the calycine squamellae, the significance of which will be treated in a subsequent paper in preparation.

DISCUSSION

This writer has been engaged for several years in the taxonomy and floral anatomy of Apocynaceae during which a majority of the generic representation of the family has been studied critically. Recourse has been had from time to time to the neighboring Asclepiadaceae as a necessary correlation. From the results of such anatomical studies, five important structural features indicate the genus *Grisebachiella* as more properly relegated to Asclepiadaceae than to Apocynaceae. Of these, the massive capitate stigmatic head with obscure, apical protrusions is a similarity easy to observe from a gross dissection. Scarcely capable of observations save from anatomical preparations are the union of the staminal filaments where they are attached to the corolla, and the bilocular condition of the anthers themselves, both characters observed in many Asclepiadaceae, and in no member of Apocynaceae known to the writer. The pollen grains, which were just breaking from the tetrads, show no tendency toward the formation of an exine and are therefore in the category of glutinous pollen, characteristic of Asclepiadaceae of the subfamily Cynanchoideae. Another technical anatomical character is the adnation of the ovary to the base of the corolla-tube. In all Apocynaceae, apparently, the ovary is subinferior, the cavities sunk in the tissues of the receptacle before the cleavage of the calyx-lobes. In this family the base of the corolla is evidently never adnate to the ovary above the receptacle.

In spite of the undeniably poor understanding of a genus possible on the basis of only three herbarium specimens, one is led to suspect that there is good biological reason for the absence of fruit. It has been found that the median trace of the carpel of *Grisebachiella* does not give rise to lateral, ovuliferous traces. The ovules themselves are lacking. Lorentz, and others who examined the specimens previously, were led to exclude the possibility of an affinity with Asclepiadaceae because of the absence of pollinia. The reason for this absence is evidently disclosed from a study of microtome sections as the result largely of the complete disorganization of the tapetal cells, the dead walls of which compose the containing membranes of the pollinia of other Asclepiadaceae (Corry, 1883). The same deficiency has evidently been responsible for the non-development of the translator mechanism. Since the pollen of Asclepiadaceae is dependent upon the mechanism of the pollinia in entomophily, the default of such leaves the pollen grains, if potent, literally imprisoned within the anthers with no means of dispersal.

While it is doubtless treading on very thin ice to dwell upon the evidence of three desiccated specimens, particularly with regard to the

peculiar tendencies which appear to be manifest in them, the fact of the rarity of the plants remains. Additional observations of the plants in the field are greatly to be desired.

SUMMARY

1. The history, morphology, and anatomy of *Grisebachiella Hieronymi* Lorentz are discussed.

2. The genus is interpreted as Asclepiadaceous rather than Apocynaceous.

3. The solitary, lateral flowers are apparently derived from a pluriflorous inflorescence.

4. An explanation, from anatomical observations of herbarium specimens, is suggested for the circumscribed distribution and insufficiently authenticated sterility of the genus.

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Recent changes in the composition of a local flora

Rogers McVaugh

In view of the interest now attaching to plant distribution, and to changes taking place in local distribution through clearing of woods, grazing, etc., it has seemed worth while to study certain early lists of plants of eastern New York State, to discover, if possible, the relations of the present local floras to those of a century ago. The following paper is an attempt to do this for the vicinity of Kinderhook, Columbia County, New York, by a study of two lists of plants published in the 52nd and 53rd Annual Reports of the Regents of the University of the State of New York (1839 and 1840), by W. V. S. Woodworth, Principal of the Ladies' Department in Kinderhook Academy.

The first list, entitled "A Catalogue of Indigenous Plants Found Growing in the Vicinity of Kinderhook Academy, and Analyzed by the Botanic Class in this Institution, during the Summer of 1838," bears the final note that "many plants had escaped notice until the most favorable season for examining them had past." The later list has essentially the same title, with the note that "the above catalogue embraces most of the plants which are found in this vicinity, and, with few exceptions, would show the botanic features of Columbia County." The second list contains about one and one-half times as many names as the first, but many of the same plants are given in both, and the two catalogues may be considered together. A total of 247 species is recorded; these are merely in the form of lists, with no data as to the plants themselves, their habitats, or the authors of the binomials. No indication is given as to methods of identification, but it seems probable that use was made of Eaton's "Manual of Botany" (7th Ed. Albany 1836), as this work was in use in a majority of the Academies of the state at the time, and the nomenclature of Woodworth's lists follows it closely.

In the following discussion, nomenclature will follow the seventh edition of Gray's Manual, with some exceptions, as published in House's "Annotated List." No attempt will be made to give the names as published by Woodworth except in the case of critical species, or where there is some doubt as to the meaning of a name; at such times the names as originally published will be given in parentheses.

The writer spent most of the summer of 1933 in the field, in and around Kinderhook, and all the species mentioned below, unless otherwise noted, are represented by herbarium specimens either in the New York State herbarium, at Albany, or in the herbarium of the University of Pennsylvania, at Philadelphia, or in both.

The village of Kinderhook is situated in the Hudson Valley, in the northwestern part of Columbia County, about five miles from the Hudson River. Its altitude is about 250 feet above sea-level. It lies on a post-glacial sand plain, which, outside the village, is now given over chiefly to apple orchards. South and east of the village runs the Kinderhook Creek, which is of some size, and drains a large part of the county; beyond the creek lies a rather hilly country with dry shaly soil. All the nearby woodland is second-growth, with no large undisturbed areas. Practically all the soil in the vicinity of Kinderhook is acid in reaction, except some of the alluvial land and swamps.

By going over the lists of Woodworth, it may be seen that about seven-eights of the species are common (or locally so) near Kinderhook at the present time. These may be placed for convenience in the following nine groups, of which the first eight represent roughly the associations in which the plants are found growing at the present day:

I. PLANTS TYPICAL OF LOW OR MOIST WOODS

Arisaema triphyllum (L.) Schott.	
Uvularia grandiflora Sm.	
Uvularia perfoliata L.	
Oakesia sessilifolia (L.) Wats.	
Erythronium americanum Ker.	
Smilacina racemosa (L.) Desf.	
Polygonatum pubescens (Willd.) Pursh	(Convallaria biflora)
Medeola virginiana L.	
Trillium erectum L.	
Hypoxis hirsuta (L.) Coville	
Cypripedium pubescens Willd.	(Cypripedium pubescens)
Habenaria psycodes (L.) Sw.	(Habernaria fimbriata)
Populus deltoides Marsh.	(Populus angulata)
Juglans cinerea L.	
Carya cordiformis (Wang.) K. Koch	(Carya amara)
Corylus americana Walt.	
Ulmus americana L.	
Ulmus fulva Michx.	
Polygonum virginianum L.	
Claytonia virginica L.	
Ranunculus abortivus L.	
Ranunculus recurvatus Poir.	(Ranunculus hirsutus)
Thalictrum dioicum L.	
Anemonella thalictroides (L.) Spach.	
Anemone quinquefolia L.	
Coptis trifolia (L.) Salisb.	

Cimicifuga racemosa (L.) Nutt.	
Actaea alba (L.) Mill.	
Actaea rubra (Ait.) Willd.	(Actea americana)
Podophyllum peltatum L.	
Sanguinaria canadensis L.	
Dentaria diphylla Michx.	
Ribes floridum L'Her.	
Geranium maculatum L.	
Zanthoxylum americanum Mill.	
Acer rubrum L.	
Impatiens biflora Walt.	
Impatiens pallida Nutt.	
Viola pubescens Ait.	
Circaea lutetiana L.	
Aralia racemosa L.	
Sanicula marilandica L.	
Nyssa sylvatica Marsh.	(Nyssa multiflora)
Collinsonia canadensis L.	
Pedicularis canadensis L.	
Galium tinctorium L.	
Solidago flexicaulis L.	
Solidago altissima L.	(Solidago canadensis)

Solidago canadensis may occur, but S. altissima is the common species here.

II. PLANTS TYPICAL OF SWAMPY OR BOGGY LAND OR MUCK

Larix laricina (DuRoi) Koch	(Pinus pendula)
Typha latifolia L.	(Typhilla latifolia)
Sagittaria latifolia Willd. var.	(Sagittaria sagittifolia)
Calla palustris L.	
Symplocarpus foetidus (L.) Nutt.	
Acorus Calamus L.	

Juncus effusus L. var. solutus Fern. & Wieg. "The common form of the species especially southward in the state—" (House).

Iris versicolor L.	
Spiranthes cernua (L.) Richard.	
Alnus rugosa (DuRoi) Spreng.	(Alnus serulata)
Polygonum arifolium L.	
Polygonum sagittatum L.	
Polygonum punctatum Ell.	
Caltha palustris L.	

Viola cucullata Ait. "In wet places . . . common throughout the state" (House).

Cicuta bulbifera L.

Cicuta maculata L.	
Cornus stolonifera Michx.	(Cornus alba)
Rhododendron viscosum (L.) Torr.	
Kalmia angustifolia L.	
Kalmia polifolia Wang.	(Kalmia glaucus)
Vaccinium corymbosum L.	
Steironema ciliatum (L.) Raf.	
Fraxinus nigra Marsh.	
Menyanthes trifoliata L.	
Scutellaria galericulata L.	(Scutellaria cordifolia)
Chelone glabra L.	
Galium trifidum L.	
Cephalanthus occidentalis L.	
Lobelia Kalmii L.	
Eupatorium perfoliatum L.	

III. PLANTS TYPICAL OF MEADOWS, USUALLY MOIST ONES

Lilium canadense L.	
Smilacina stellata (L.) Desf.	
Polygonatum commutatum (R. & S.) Dietr.	
Sisyrinchium gramineum Curtis.	(Sisyrinchium anceps)
Anemone canadensis L.	
Penthorum sedoides L.	
Saxifraga pennsylvanica L.	
Geum rivale L.	
Spiraea latifolia Borkh.	(Spirea salicifolia)
Spiraea tomentosa L.	
Veronica virginica L.	

IV. PLANTS GROWING IN LAKES AND PONDS

Pontederia cordata L.
Castalia odorata (Ait.) W. & W.
Nymphaea advena Ait.

V. PLANTS OF STREAM BANKS

Ranunculus repens L.	
Platanus occidentalis L.	
Acer saccharinum L.	(Acer dasycarpum)
Teucrium canadense L.	
Stachys tenuifolia Willd. var. aspera (Michx.) Fern.	
Lycopus americanus Muhl.	(Lycopus europeus)
Mimulus ringens L.	
Veronica americana Schwein.	(Veronica anagallis)
Lobelia cardinalis L.	

VI. PLANTS OF OPEN WOODS AND THICKETS

Smilax herbacea L.
Populus tremuloides Michx.
Polygonum scandens L.
Phytolacca americana L.
Clematis virginiana L.
Fragaria virginiana Duchesne
Geum virginianum L.
Rosa carolina L. (Rosa parviflora) "Frequent or common, outside the higher Adirondacks, across the state" (House).
Rubus idaeus L. var. aculeatissimus (Mey.) R. & T. (Rubus strigosus)
Rubus occidentalis L.
Rubus sp.? No doubt a high-bush Blackberry. (Rubus villosus)
Prunus virginiana L.
Epilobium angustifolium L.
Vaccinium vacillans Kalm.? (Vaccinium virgatum)
Vaccinium pennsylvanicum Lam.? (Vaccinium tenellum)
Cuscuta Gronovii Willd. (Cuscuta americana)
Verbena hastata L.
Verbena urticaefolia L.
Diervilla Lonicera Mill.
Sambucus canadensis L.

VII. PLANTS OF DRY WOODS

Pinus rigida Mill.
Pinus resinosa Ait.
Pinus Strobus L.
Tsuga canadensis (L.) Carr. (Pinus canadensis)
Maianthemum canadense Desf.
Epipactis pubescens (Willd.) A. A. Eaton.
Carya ovata (Mill.) K. Koch (Carya alba)
Ostrya virginiana (Mill.) K. Koch
Betula lenta L.
Betula lutea Michx. f.
Fagus grandifolia Ehrh.
Castanea dentata (Marsh.) Borkh.
Quercus alba L.
Quercus velutina Lam.
Hepatica americana (DC.) Ker.
Anemone virginiana L.
Aquilegia canadensis L.
Sassafras variifolium (Salisb.) Ktze.
Saxifraga virginiensis Michx.

Mitella diphylla L.
Hamamelis virginiana L.
Amelanchier canadensis (L.) Medic. (Aronia botryapium)
Prunus serotina Ehrh.
Acer pennsylvanicum L.
Acer saccharum Marsh. (Acer saccharinum)
Tilia americana L.
Aralia nudicaulis L.
Osmorhiza longistylis (Torr.) DC. (Uraspermum claytonia)
"Frequent or common northward across the state." (House).
Cornus canadensis L.
Cornus florida L.
Chimaphila umbellata (L.) Nutt.
Pyrola americana Sweet.
Monotropa uniflora L.
Rhododendron nudiflorum (L.) Torr.
Gaultheria procumbens L.
Gaylussacia baccata(Wang.) Koch (Vaccinium resinosum)
Lysimachia quadrifolia L.
Trientalis americana (Pers.) Pursh
Fraxinus americana L.
Asclepias quadrifolia Jacq.
Hedeoma pulegioides (L.) Pers.
Aureolaria virginica (L.) Pennell (Gerardia flava)
Veronica officinalis L.
Galium lanceolatum Torr.
Mitchella repens L.
Sambucus racemosa L.

VIII. PLANTS OF DRY FIELDS

Pteridium latiusculum (Desv.) Maxon.
Equisetum hyemale L. var. (Equiseum hyemale)
Juniperus virginiana L. (Juniperus cinerea)
Spiranthes gracilis (Bigel.) Beck.
Betula populifolia Marsh.
Rubus villosus Ait. ? Dewberry. (Rubus trivialis)
Baptisia tinctoria (L.) R. Br.
Lupinus perennis L.
Oxalis stricta L.
Oenothera biennis L.
Apocynum androsaemifolium L.
Asclepias amplexicaulis Sm.
Asclepias syriaca L.
Isanthus brachiatus (L.) BSP.

Solanum nigrum L.
Penstemon hirsutus (L.) Willd.
Lobelia inflata L.
Krigia virginica (L.) Willd.

IX. INTRODUCED SPECIES: MOSTLY WEEDS

Populus nigra L. var. italica DuRoi.	(Populus dilatata)
Ulmus campestris L.	
Rumex Acetosella L.	
Polygonum Persicaria L.	
Fagopyrum esculentum Moench.	
Agrostemma Githago L.	
Ranunculus acris L.	
Chelidonium majus L.	
Robinia Pseudo-Acacia L.	
Aesculus Hippocastanum L.	
Hypericum perforatum L.	(Hypericum perfoliatum)
Conium maculatum L.	
Ligustrum vulgare L.	
Lithospermum arvense L.	
Nepeta Cataria L.	
Prunella vulgaris L.	
Lamium amplexicaule L.	
Datura Stramonium L.	
Verbascum Thapsus L.	
Linaria vulgaris Hill.	
Veronica agrestis L.	
Tecoma radicans (L.) Juss.	(Bignonia trumpicans)
Inula Helenium L.	
Achillea Millefolium L.	
Chrysanthemum Leucanthemum L. var.	
Arctium minus Bernh.	(Arctium lappa)
Cirsium arvense (L.) Scop.	
Cirsium lanceolatum (L.) Hill.	
Taraxacum officinale Weber.	

About one-half of the remaining species are plants no longer found, so far as known, in the vicinity of Kinderhook:

Abies balsamea (L.) Mill.	(Pinus balsamea)
Lilium philadelphicum L.	
Lilium superbum L.	
Smilacina trifolia (L.) Desf.	(Convallaria trifolia)
Cypripedium arietinum R. Br.	
Habenaria flava (L.) Gray	(Orchis flava)

Habenaria orbiculata (Pursh) Torr.	
Juglans nigra L.	
Rubus setosus Bigel.	
Oxalis Acetosella L.	
Hippuris vulgaris L.	
Rhododendron maximum L.	(Azalea arborescens)
Kalmia latifolia L.	
Gaylussacia dumosa (Andr.) T. & G.	(Vaccinium dumosum)
Gaylussacia frondosa (L.) T. & G.	(Vaccinium frondosum)
Convolvulus Sepium L. var. pubescens (Gray) Fern.	(Convolvulus repens)
Houstonia caerulea L.	
Campanula americana L.	
Cirsium altissimum (L.) Spreng.	

To complete the list we have (a) five species, which, if they ever grew here, were no doubt introductions, and are not now known to grow in Kinderhook:

Taxodium distichum (L.) Richard	(Cupressus disticha)
Chamaecyparis thyoides (L.) BSP.	(Cupressus thyoides)
Belamcanda chinensis (L.) DC.	(Ixia chinensis)
Indigofera tinctoria L.	
Sida spinosa L.	

and (b) eight names which are too doubtful in their application to be made use of in this paper. They include those cases in which synonymy is obscure or in which a name seems to have been wrongly applied to a plant which grew in the area under discussion:

Convallaria latifolia
Arenaria glabra
Arenaria serphyllum
Arenaria stricta
Cerastium hirsutum
Cerastium semidecandrum
Crategus coccinea
Oenothera parviflora

CONCLUSION

Since about seven-eights of the species mentioned by Woodworth are seen to be common or locally so about Kinderhook at the present time, we may conclude that no great changes have taken place in the flora during the last century. This is borne out by the fact that numbers of species in the arbitrary habitat groupings which the writer has made above agree very well with relative numbers of species in the same habi-

tats today. The above conclusion is perhaps to be expected, since the village was settled by the Dutch about 1640, and reference to old maps and deeds shows that farm boundaries have existed, much as they are at present, for many years. The greatest single change in the aspect of the vegetation has been in the cutting of several small areas of first-growth timber, mostly White Pine and Hemlock, some of which was standing as late as 1900.

A closer study of Woodworth's list, however, seems to indicate that the northern or high-altitude elements of the flora were more pronounced formerly than now; the following selection of plants noted by Woodworth consists of those species having decidedly northern affinities, or, in this part of the Hudson Valley, typical of cold bogs or the elevations of the Taghkanic Mountain region to the eastward:

*Pinus resinosa Ait.
*Larix laricina (DuRoi) Koch
Abies balsamea (L.) Mill.
*Calla palustris L.
Lilium philadelphicum L.
Smilacina trifolia (L.) Desf.
Cypripedium arietinum R. Br.
Habenaria flava (L.) Gray
Habenaria orbiculata (Pursh) Torr.
*Coptis trifolia (L.) Salisb.
Rubus setosus Bigel.
Oxalis Acetosella L.
*Acer pennsylvanicum L.
*Epilobium angustifolium L.
Hippuris vulgaris L.
*Cornus canadensis L.
Kalmia latifolia L.
*Kalmia angustifolia L.
*Kalmia polifolia Wang.
*Menyanthes trifoliata L.
Houstonia caerulea L.

At the present time none of the above species is even locally common near Kinderhook; the ten marked with a star are rare in the vicinity and the rest are unknown. The ten species now growing here are known from only two to three stations at most. Accordingly it seems probable that the plants in the above short list occupied a somewhat more prominent place in the flora of a hundred years ago than they do now, if they were all to be recorded in a catalogue which is made up mostly of fairly common

plants. These species may have found conditions favorable to their growth in the deeper, colder forests of which only the stumps remain; forests which still persist to some extent in the more thinly settled portions of Columbia and Rensselaer counties, and in which are found in more or less abundance most of the plants noted above.

It also seems worth while to add a short list of species, now rare or unknown in the vicinity of Kinderhook, which may have been frequent or occasional in their occurrence at the time of Woodworth. This is largely speculative, but is in part supported by ranges of species as published in the manuals, and by references to various species by authors of local floras such as Hoffmann, Hoysradt, Stebbins, Wright and Hall, and others:

Uvularia grandiflora Sm.
Lilium superbum L.
Epipactis pubescens (Willd.) A. A. Eaton
Juglans nigra L.
Lupinus perennis L.
Nyssa sylvatica Marsh.
Rhododendron maximum L.
Gaylussacia dumosa (Andr.) T. & G.
Gaylussacia frondosa (L.) T. & G.
Convolvulus Sepium L. var. pubescens (Gray) Fernald.
Isanthus brachiatus (L.) BSP.
Campanula americana L.
Cirsium altissimum (L.) Spreng.

No effort has been spared to prevent errors in transcribing the above catalogues, but some have undoubtedly crept in. While such an article as the present one is largely of local interest, it is felt that it shows the general trend of plant associations well enough to merit general publication. In the preparation of the manuscript the writer has availed himself of the help of several friends, and he wishes especially to thank Dr. Homer D. House, the State Botanist of New York, and Dr. John M. Fogg, of the University of Pennsylvania, for their generous assistance at all times.

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Fusarium crown and root rot, and Sclerophoma stem blight, of the Texas bluebell[1]

J. J. Taubenhaus and Walter N. Ezekiel

(with two text-figures)

The Texas bluebell, *Eustoma russellianum*, is a native perennial growing in low meadows in calcareous soils in many sections of East and North Central Texas. In recent years, the Texas bluebell has been taken into cultivation in limited areas near some of the larger cities of Texas, yet market supplies of the blooms of this plant are still limited. Many florists who have attempted to grow this plant have become discouraged on account of attacks of various diseases. There is, ordinarily, little or no loss from disease in new plantings. Diseases appear usually during the second year and become progressively worse as the plants are grown continuously in the same place. For instance, a grower of Dallas, Texas,[2] started out in 1931 with about a thousand Texas bluebells and experienced no loss from disease during that year. But by the end of the next year, 80 per cent of the plants were dead. Plantings of Texas bluebells near San Antonio, Houston, and Beaumont have similarly shown annual losses from disease of only 15 to 30 per cent in new plantings, while in the older plantings losses ranged from 50 to 100 per cent.

It may be noted that in a wild state, Texas bluebells suffer relatively little from diseases. Large colonies of these plants have been examined near Madisonville. In 1932, of 500 plants examined, 3.5 per cent were dead or in a dying condition; and in 1933, of 500 plants examined, 5.3 per cent were dead or dying.

Of the several diseases of the Texas bluebell plant only two have been given attention.

I. Fusarium crown and root rot

Seedlings as well as older Texas bluebells develop a destructive crown and root rot. In the early stages of this disease, watersoaked areas appear on the crown of the plant, just above the surface of the ground. These areas enlarge, become depressed, and extend downward into the roots, which soften and decay. Meanwhile, the tops of the plants wilt, collapse, and die. During moist weather, the crowns of diseased plants become covered with scattered pinkish masses of *Fusarium* spores. Affected plants

[1] Published with the approval of the Director as Contribution No. 303, Technical Series, Texas Agricultural Experiment Station.

[2] The writers are indebted to Mr. G. M. Soxman, of Dallas, Texas, who has provided material for these studies, and has carried out the program of experimental spraying.

[The Bulletin for November (62: 433–565) was issued November 1, 1935]

succumb usually within a few days and rarely if ever recover from this disease.

Plants giving evidence of this disease were received first in 1931 from plantings at Dallas, Texas. Cultures were made from small, surface sterilized portions of infected root and stem tissues. *Fusarium*, *Trichoderma*, *Rhizoctonia*, and *Alternaria* were recovered from the infected root and stem material. Pure cultures of each fungus were grown on potato-dextrose agar slants and used to inoculate five normal Texas bluebell plants growing in steam-sterilized soil in 4-inch pots, while a similar number of plants in other pots were left as uninoculated checks. The entire fungus growth in two agar slants was placed next to the crown of each plant to be inoculated and covered with moist non-absorbent cotton. Plants inoculated with the *Fusarium* succumbed (fig. 1, a), reproducing typical crown and root rot; while the non-inoculated check plants, and those inoculated with *Trichoderma* or *Alternaria*, remained healthy. The plants inoculated with *Rhizoctonia* developed deep cankers, at the foot of the plant, quite unlike the root and crown rot caused by the *Fusarium*.

The *Fusarium* thus proved to cause crown and root rot of Texas bluebells was identified as *Fusarium solani*, and this identification verified by Dr. C. D. Sherbakoff. *Fusarium solani* has already been shown to cause in Texas a crown and root rot of spinach,[3] and a serious crown and corm decay of freesias.[4]

II. SCLEROPHOMA STEM BLIGHT

The second and more important disease of Texas bluebells is a stem blight which may occur also on the leaves. This trouble was found prevalent in every planting of Texas bluebells under cultivation near Dallas, Houston, and San Antonio, Texas. It attacks mature as well as young plants and is much more destructive during the second year than during the year following planting.

Stem blight becomes evident at the crown of the plant involving the main stem, and at the same time usually produces independent small, whitish, depressed lesions on the leaves and lateral branches of the plant. On leaves, the lesions usually enlarge; but if numerous they remain small and coalesce. Damage to the leaves is unimportant compared to the injury to the main stem. Here the infection rapidly spreads upward from the crown, and meanwhile extends around the stem. As the stem is gir-

[3] Taubenhaus, J. J. 1926. Studies of a new *Fusarium* wilt of spinach in Texas. Texas Agr. Expt. Sta. bull. 343: 5–23.

[4] Taubenhaus, J. J., and Ezekiel, Walter N. 1933. *Fusarium* wilt and corm rot of freesias. Botan. Gazette 95: 128–142.

dled, first the lower leaves of the plant wilt, and within a few days all the leaves have wilted, whitened, and begun to shrink (fig. 1, c and d). Within three to ten days of infection, numerous scattered pycnidia appear as dark

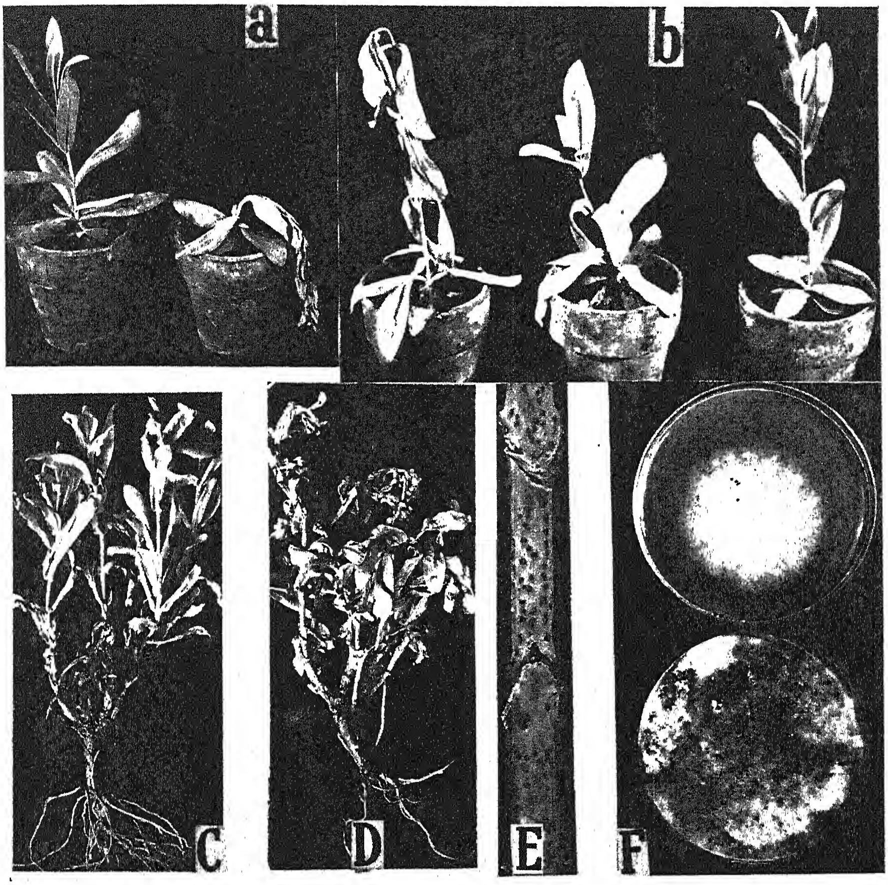

Fig. 1. Inoculation experiments with Texas bluebell plants; a, inoculation with *Fusarium solani*, left, uninoculated plant, and right, one inoculated plant; and b, right to left, progressive decline of plants inoculated with *Sclerophoma eustomonis;* c, early and d, advanced stage of plants naturally infected by *Sclerophoma* blight; e, pycnidia of *S. eustomonis* appearing on stem of naturally infected plant; f, cultures of *S. eustomonis* in Petri dishes of potato-dextrose agar.

specks on the diseased areas, first near the crown, and then progressively upward along the main stem and laterals (fig. 1, e). Pycnidia are rarely found on the leaves although the fungus has been isolated successfully from the whitish lesions on the leaves. When placed in a moist chamber,

the spores ooze out from the pycnidia as small irregular creamy tendrils or droplets.

After the top of the plant has succumbed, new shoots sprout from below the injured portion, grow into sound stems, and may even yield a crop of blooms. Ultimately, these secondary shoots are attacked and killed

TABLE 1

Inoculation of Texas bluebells with Sclerophoma eustomonis.

(Plants growing in 4-inch pots in steam sterilized soil, 1 plant per pot, 5 plants per series).

DATE OF INOCULATION	INOCULUM	METHOD OF INOCULATION	PER CENT INFECTION AFTER 3 WEEKS
2–23–33	Suspension of pycniospores of *Sclerophoma eustomonis* from an infected stem of a Texas bluebell plant	Spores sprayed with atomizer on leaves and stems. Inoculated plants kept for 12 hours under moist bell jars	100[1]
—	Check	Not inoculated	0
4– 5–33	Suspension of pycniospores of *Sclerophoma eustomonis* from a pure culture growing on sterilized Texas bluebell stems	Spores sprayed with atomizer on leaves and stems. Inoculated plants kept for 12 hours under moist bell jars	100[1]
do	Pure culture of *Sclerophoma eustomonis* isolated from an infected stem of a Texas bluebell plant	Two tube cultures worked into soil around each plant, then covered with non-absorbent cotton	80[1]
—	Check	Not inoculated	20[2]
5– 2–33	Pure culture of *Sclerophoma eustomonis* recovered from *Pseudococcus maritimus* insects secured from an infected bluebell plant	Two tube cultures worked into soil around each plant, then covered with non-absorbent cotton	80[1]
—	Check	Not inoculated	0

[1] Organism recovered from 2 of the inoculated plants in each series.
[2] One check plant showed lesions and pycnidia of *S. eustomonis* on a small branch.

also. Usually no more new shoots are produced, and the roots of the plants are now attacked by various other organisms, particularly *Fusarium solani*.

Cultures made from bits of infected leaf or stem tissue yielded uniformly pure cultures of a fungus identified by Dr. C. L. Shear as a species of *Sclerophoma*.

A number of normal 3-months-old Texas bluebell plants growing in

pots in steam-sterilized soil were inoculated with a pure culture of this *Sclerophoma*. The methods of inoculations and the results are indicated in table 1. The typical stem and leaf blight was successfully reproduced by

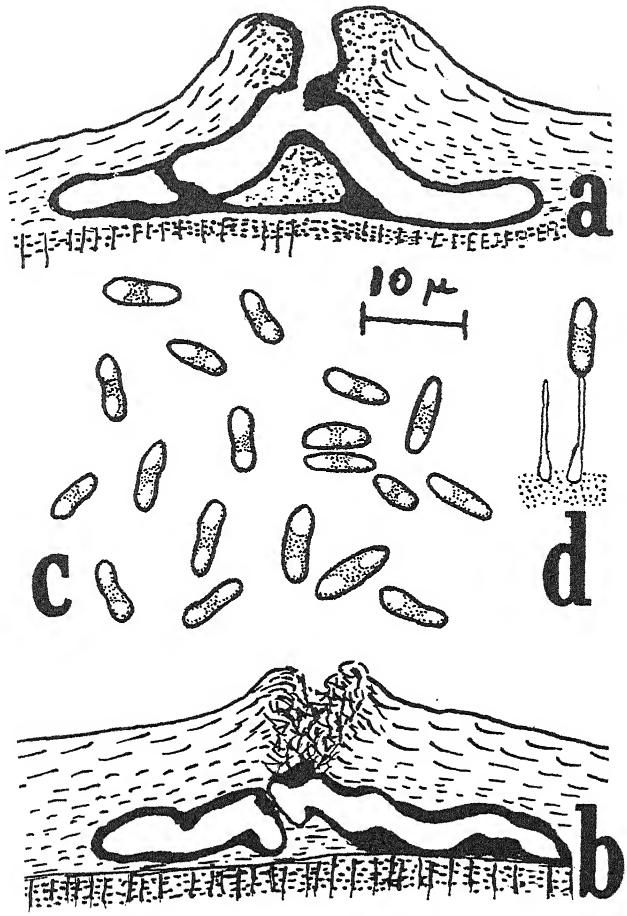

Fig. 2. a and b, sections of pycnidia of *Sclerophoma eustomonis* (diagrammatic); c, individual pycniospores; d, pycniospore attached to conidiophore. (a and b drawn by L. B. Loring, c and d drawn by Ezekiel)

all methods of inoculation, while almost all of the check plants remained normal (fig. 1, b).

The *Sclerophoma* sp. which affects Texas bluebells appears to be a new species, and the name *Sclerophoma eustomonis* Taubenhaus and Ezekiel was tentatively given to this organism.[5,6]

Sclerophoma eustomonis Taubenhaus and Ezekiel, sp. nov. Pycnidia dark, flattened, lenticular, imbedded, in a stromatic layer in host cortical tissue; 135 to 300μ in diameter, by 85 to 145μ in depth. Some with pycnidial wall only slightly irregular, forming single locules; others with the wall quite irregular and extensively lobed, dividing pycnidia into several locules, separated by the heavy folds of the pycnidial wall, as shown in figure 2, a and b. Conidia borne on small sporophores with extremely minute, nearly invisible, tips (fig. 2, d). Spores cylindric, 1-celled; hyaline, almost always with two conspicuous droplets, one near each end of spore, occasionally with only a single droplet near center of spore (fig. 2, c); mean size $6.8 \times 2.46\mu$, range $4.5-8.7 \times 2.1-3.1\mu$.

Fungi pycnidiis in lamellis stromatibus in hospitis thallo immersis; fuscis, applanatis, lenticulatis, unipluriloculatis; 135–300μ crassis, 85–145μ altis. Conidiophorae parvulae, apiculatae; conidia cylindracea, continua, hyalina, saepe 2-guttulata; $4.5–8.7 \times 2.1–3.1\mu$; vulgo $6.8 \times 2.46\mu$.[7]

The fungus is readily isolated and grows rapidly on potato-dextrose agar. Colonies are at first thin, somewhat fluffy and whitish, but after two weeks become flat, compact, brown and leathery, with the lower surface distinctly wrinkled. After about three weeks, dark brown stromatic pycnidial clumps begin to appear on the surface of Petri dish or tube cultures (fig. 1, f) and mature in six to ten weeks.

The fungus is parasitic on Texas bluebells. Type material and pure cultures of the fungus have been deposited with the Centraal-Bureau voor Schimmelcultures and with the United States National Museum.

Sclerophoma stem lesions frequently occur on the peduncles or on the seed pods of the affected plants. The seeds of Texas bluebells are minute and shatter readily as soon as the seed pods mature and dry. For this reason, the seed pods are harvested in a somewhat green condition, and allowed to dry in paper sacks. At planting time the pods are broken by hand, and infected seed pod tissue may thus become mixed with the seed. To check the possibility of the disease being carried in this way, unscreened and unsterilized seeds from Texas bluebell plants infected by *Sclerophoma* blight were planted in steam sterilized soil. The resultant plants were isolated and protected from chance infection, yet 140 of about 500 seedlings developed *Sclerophoma blight.*

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[5] Taubenhaus, J. J., and Ezekiel, W. N. On a new root rot and stem blight of Texas bluebells, *in* Texas Agr. Expt. Sta. Ann. Rept. 45: 77. 1932. (in this report, the name of the fungus was misspelled as *Sclerophoma customonis*).

[6] Taubenhaus, J. J., and Ezekiel, W. N. Check list of diseases of plants in Texas. Trans. Texas Acad. Sci. 16: 5–89, 101–118. (p. 31) 1933.

[7] The writers are indebted to Dr. O. M. Ball for preparing this Latin diagnosis.

Texas bluebell plants are commonly attacked by a mealy bug identified as *Pseudococcus maritimus*.[8] Over three hundred mealy bugs were secured directly from plants affected also by *Sclerophoma* blight. The insects were transferred carefully with sterilized forceps to Petri dishes of potato-dextrose agar. Pure cultures of *Sclerophoma* were recovered from 4 per cent of the mealy bugs thus cultured, and the fungus successfully inoculated on normal Texas bluebell plants. Viable *Sclerophoma* spores were recovered also by centrifuging, in sterilized water, mealy bugs secured from infected plants. These results support the conclusion that mealy bugs may spread *Sclerophoma* blight by pycniospores which adhere to the bodies of these insects. Red spider, *Tetranychus bimaculatus* Harw., also attacks bluebell plants and may be concerned in spread of this disease.

CONTROL OF SCLEROPHOMA BLIGHT

Mature seed pods were secured from naturally infected bluebell plants. The seed pods were then broken up, and the minute seed were screened out and separated from the pod debris. The seed were dipped for 5 minutes in a solution of 1–2000 bichloride of mercury in 25 per cent alcohol, and planted in steam-sterilized soil. No disease appeared on the young seedlings from the seed thus treated. On the other hand, considerable *Sclerophoma* blight appeared on a number of the seedlings from the screened seed that was not disinfected, and on those from the seed that was neither screened nor disinfected.

A number of spraying programs were tested by Mr. G. M. Soxman of Dallas, Texas. During 1931, the plants were sprayed with 4-4-50 Bordeaux with little success. This was explained by the natural gloss of the plant which prevented adherence of the spray. During 1932, casein was added which increased the adhesiveness of the Bordeaux, but gave only slightly better control. During 1932, casein and also nicotine sulphate were added to the Bordeaux. This combined fungicide and insecticide adhered well and reduced *Sclerophoma* blight to 20 per cent in the sprayed plants, while unsprayed plants were practically a total loss.

During 1930, Mr. Soxman made successful crosses of Texas bluebells from North and South Texas. Of the twenty-five plants raised, twenty-four had typical large leaves and were susceptible to *Sclerophoma* blight. The remaining plant had narrow leaves and appeared resistant to stem and leaf blight. Progeny of this plant continue to maintain high resistance to *Sclerophoma* blight, but some of the strains have produced abnormal sterile plants.

[8] Identified by Dr. C. A. Weigel, of the Bureau of Entomology, U. S. Department of Agriculture.

SUMMARY

Attempts by florists to grow the Texas bluebell under cultivation have been disappointing because of the attacks of numerous diseases. The present paper deals with two of these diseases. A crown and root rot of seedlings and older plants was proved due to *Fusarium solani*. A second and more destructive disease is a stem blight caused by *Sclerophoma eustomonis* n.sp., a description of which is given. Mealy bugs (*Pseudococcus maritimus*), were proved capable of spreading the causal organism. Sclerophoma is carried by fragments of infected pods mixed with the seeds, and sterilizing the screened seeds lowered infection. A combination spray of Bordeaux, nicotine sulphate, and casein gave fair control of the blight. A strain of Texas bluebells with narrow leaves has shown high resistance to *Sclerophoma* blight, but has not yet been stabilized as to horticultural characteristics.

TEXAS AGRICULTURAL EXPERIMENT STATION,
COLLEGE STATION, TEXAS

Three new cuscutas

T. G. Yuncker

(with one text-figure)

Cuscuta yucatana n. sp.

Caules tenues. Flores circ. 2 mm. longi. Pedicellati aequantes aut longiores quam flores. Calycis lobi triangulari-ovati, acuti. Corollae lobi oblongo-lanceolati, acutissime acuti, aequantes aut longiores quam corollae tuba campanulata, apices plus aut minus inflexi. Scalae oblongae aut plus aut minus spatulatae. Filamenta tenua aut plus aut minus subulata et longiora quam antherae oval-ellipticae. Styli tenui, aequantes aut longiora quam ovarium depresso-globosum. Capsula globoso-depressa, obovoida, non circumscissilis, corolla marcescens circum partem inferiorem. Semina 0.8–1.0 mm. longa.

Stems slender. Flowers about 2 mm. long, soon appearing larger because of the developing capsule, on pedicels as long as or more commonly somewhat longer than the flowers, in compound, umbellate cymes. Calyx longer than the corolla tube, lobes triangular-ovate, acute, not overlapping at the base. Corolla lobes oblong-lanceolate, very sharply acute, upright in young flowers, tips inflexed, soon becoming reflexed about the developing capsule, as long as or more commonly longer than the campanulate tube, more or less granular-papillate. Filaments slender to slightly subulate, mostly two to three times as long as the oval-elliptical anthers. Scales oblong or slightly spatulate, reaching the stamens, fringed with medium length processes, bridged at about one-fourth their height. Styles equal to or longer than the depressed-globose ovary. Capsule globose-depressed, more or less obovoid, comparatively large and bulging about the enclosed seeds, not circumscissile but thin towards the base and when torn away leaving the obcordate dissepiment in the calyx, withered corolla remaining about the lower part; seeds generally four in each capsule, mostly 0.8–1.0 mm. long, oval, hilum slightly oblique.

This species belongs in Subsection Acutae of Section Cleistogrammica with those species having acute flower parts and in which the capsules do not open by a definite circumscission. It would seem to be best placed between *C. globosa* Ridley of Brazil and *C. acuta* Engelmann of the Galapagos Islands. From *C. pentagona* Engelmann and *C. campestris* Yuncker it differs because of the longer pedicels and consequently less compact inflorescences, as well as by the acute calyx lobes. It appears to be most closely related to *C. acuta* but differs from that species chiefly in its smaller flowers and longer pedicels, as well as in the shape of its capsules.

SOUTHEASTERN MEXICO: Valladolid, Yucatan, *W. C. Steere*, July 2, 1932 (*No. 1695*), the type, in the Field Museum of Natural History.

Cuscuta deltoidea Yuncker var. **serrulata** n. var.

Calycis lobi serrati et plus aut minus acuti. Corollae lobi inserrati aut serrati.

The calyx lobes of this variety are coarsely and irregularly serrated and are somewhat more pointed than those of *C. deltoidea*. The corolla lobes are entire or shallowly and irregularly serrated. Otherwise this variety closely resembles the species.

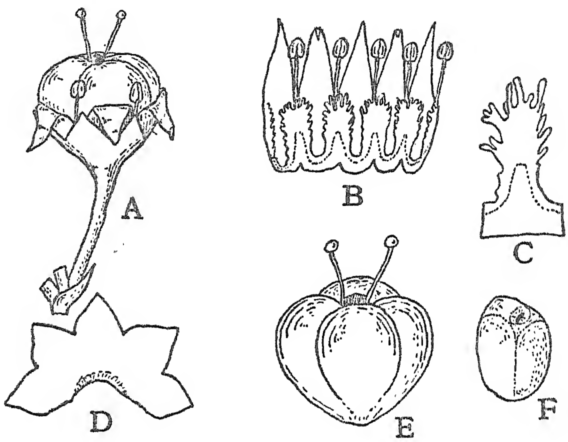

Fig. 1. *Cuscuta yucatana* n. sp. A, flower ×6; B, opened corolla ×6; C, individual scale ×12; D, opened calyx ×6; E, capsule ×6; F, seed ×10.

The size of the flowers, the shape of the calyx lobes, the length of the stamens, which are about as long as the corolla lobes, and characteristics of the flowers in general more closely ally this variety with *C. deltoidea* than with *C. gracillima* Engelmann. The shape and proportion of the calyx and corolla lobes distinguish it from *C. lacerata* Yuncker.

WESTERN MEXICO: Manzanillo, State of Colima, *C. R. Orcutt*, Oct. 20, 1919, the type, in the Field Museum of Natural History. (This is also the type locality of *C. deltoidea*.)

Cuscuta Suksdorfii Yuncker var. **subpedicellata** n. var.

Flores sessiles aut subsessiles, 2.0–3.0 mm. longi. Calycis lobi triangulari-acuti, longiores quam corollae tuba, breviores quam stamina. Capsula globosa aut globoso-depressa.

Flowers sessile or subsessile, 2–3 mm. long. Calyx lobes triangular, acute, exceeding the corolla tube, but not exceeding the stamens. Capsule globose or depressed globose.

The flowers of *C. Suksdorfii* are mostly definitely stalked and with the calyx lobes long, slenderly attenuated, and generally extending much beyond the stamens, and with capsules globose to ovoid.

NORTHERN CALIFORNIA: Siskiyou Mts., Siskiyou County, Head of E. Fork Horse Creek, 6500 ft. alt., on *Calyptridium umbellatum*, *Louis C. Wheeler*, Aug. 21, 1934 (*No. 3192*), the type: One mile E. Dry Lake Lookout, 6000 ft. alt., on the same host species, *Louis C. Wheeler*, July 31, 1934 (*No. 3011*). Both specimens in the writer's herbarium.

DePauw University,
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Angiosperm phylogeny on a chemical basis

JAMES B. MCNAIR

(WITH FIVE TEXT-FIGURES)

It is proposed in this paper to consider some phylogenetic theories relating to the angiosperms in the light of chemical analysis. Plants can be classified chemically in accordance with the substances made by them. Such a chemical classification may be compared with or used as a supplement to morphological classification and may be of some importance in the development of the true natural system of angiosperm phylogeny.

USE OF CHEMICAL FACTORS IN THE STUDY OF PHYLOGENY

In this paper some physical and chemical properties of alkaloids, glycerides (fats) and volatile oils are used in the comparison of plant families and orders as well as in the comparison of different plant groups, e.g. the monocotyledons with the dicotyledons. In a previous publication (McNair, 1934) it has already been shown, first, that the more closely plants are related, the more closely similar are their chemical products; and second that the more highly evolved the plant (according to the Engler and Gilg classification) the larger are the molecules of its chemical products provided that the plants grow in the same climate. These findings will be made use of here in further comparisons of angiosperm phylogeny.

The chemical findings produce further information as to both the Bessey and the Engler and Gilg systems of classification. They show that in the glycerides the iodine numbers increase with the evolution in plant groups such as orders, etc. Space does not permit the inclusion here of all the tables from which the data in this paper were obtained. The average molecular weights for the alkaloids of the various plant families, the average familial iodine numbers of the glycerides, the average familial specific gravities of the volatile oils and the average refractive indices of the volatile oils used in this paper were secured from McNair (1934).

The arrangement of families and orders in the Bessey system is to be found in Bessey (1914), and the arrangement of families and orders in the Engler and Gilg system has been taken from Engler and Gilg (1919).

In the discussion of results obtained in this paper from tables Nos. 3 to 6 inclusive, the first column on the left includes all the tropical families from which data have been obtained, while the other columns include only part of these families. Therefore the left hand column gives a better average value founded on a larger group of plant families than any of the other columns. The figures in it can consequently be considered as more representative and dependable than those in the other columns.

The alkaloids increase in molecular weight in proportion to their increase in plant evolution (McNair, 1934). This is strikingly shown in the present paper in the consideration of Magnoliaceae vs. Ranunculaceae, herbs vs. trees, dicotyledons vs. monocotyledons, polypetaly vs. gamopetaly, and polycarpy vs. oligocarpy.

In apocarpy vs. syncarpy, the results do not coincide with those obtained by the use of the glycerides and volatile oils. In this instance, however, there is only a slight difference between the alkaloid values, e.g. 333 vs. 308 is 7.5%.

In the study of volatile oils, the specific gravities show that these values increase in general with plant evolution in the small as well as in the large plant groups. The refractive indices, however, decrease as evolution increases. This is in accordance with the general rule previously developed (McNair, 1932) that a lowering in the index of refraction carries with it an accompanying increase in the specific gravity.

ARE THE MAGNOLIACEAE PRE-RANUNCULACEAN?

Hallier (1905a, b) believed that the Ranunculaceae and Nymphaeaceae are descended from the Magnoliaceae through the Schizandraceae, Lardizabalaceae and Berberidaceae.

Engler, however, has concluded that it is not likely that such characteristically woody families as the Magnoliaceae and Lauraceae have arisen from herbaceous ancestors, or vice versa, but that these woody types have had a quite different origin from the herbaceous Ranunculaceae, as have most of the monocotyledons whose protangiospermous ancestors may be assumed to have been herbaceous (Campbell, 1930).

Volatile oils have been found in the Ranunculaceae, alkaloids in the Ranunculaceae and Berberidaceae, and glycerides in the Ranunculaceae, Berberidaceae and Lardizabalaceae. All three of these families are found for the most part in the temperate zone and consequently they can be successfully compared chemically. The accompanying table 1 shows that the values of the alkaloids diminish from the Ranunculaceae to the Berberidaceae; and that the values of the glycerides diminish correspondingly

TABLE 1

Are the Magnoliaceae pre-ranunculacean?

FAMILY	DOMINANT FORM	ALKALOIDS (MOL. WT.)	GLYCERIDES (IOD. NO.)
Magnoliaceae	Shrub-Tree	—	95.5
Lardizabalaceae	Shrub	—	78.4
Berberidaceae	Herb-Shrub	330	139.1
Ranunculaceae	Herb	543	145.0

from the Ranunculaceae, through the Berberidaceae to the Lardizabalaceae. Consequently, Hallier's theory of descent has chemical support as far as chemical data are available.

The Ranunculaceae consist mainly of herbs, the Berberidaceae of herbs and shrubs, and the Lardizabalaceae of shrubs. Here there is an indication that shrubs may precede herbs phylogenetically.

The Magnoliaceae are mainly a sub-tropical family and therefore can not be compared chemically with the three temperate zone families considered here. The average iodine number of the glycerides of the Magnoliaceae, 95.5, should be lower than the temperate glycerides and higher than the tropical glycerides in order to comply with the general rule. Assuming that the Magnoliaceae are plants of the temperate zone as are the three other families, their low value, 95.5, would indicate that they are more primitive than the Berberidaceae and Ranunculaceae.

ARE HERBS DERIVED FROM TREES?

The foregoing chemical results indicate that herbs may be derived from trees. Eames (1911), in a paper devoted to the subject, brings forward evidence that the earliest dicotyledons possessed a solid tubular woody cylinder of considerable thickness which has gradually been reduced, and finally broken up into a circle of separate strands, which is characteristic of the "typical" herbaceous condition. Such an hypothesis of reduction from primitive arborescent forms has also been worked out under the direction of Professor Jeffrey by several other members of his laboratory (Adkinson, 1913, Bailey, 1911, and Jeffrey, 1912). In more recent papers, Sinnott and Bailey, (1914, 1922), produced evidence in support of this view from palaeobotany, phylogeny, anatomy and geographical distribution. It is no wonder then that Bessey (1915) included in his "General principles adopted for the classification of plants" the postulate that "in certain groups, trees and shrubs are probably more primitive than herbs."

This hypothesis may be considered from the standpoint of the chemical products derived from plants. In table 2, the glycerides, alkaloids, and volatile oils from tropical plant families are considered in this respect.

From the final average obtained of the molecular weights of the alkaloids, there is a clear indication that trees produce alkaloids of lower molecular weights than shrubs, and that shrubs have lower alkaloid averages than herbs. Corresponding results are obtained from the iodine numbers of glycerides. The average refractive indices and specific gravities of volatile oils in respect to the dominant form of plant growth in the families is also developed in table 2. Here again the findings clearly indicate that trees may be the ancestors of herbs. This is shown in the specific gravities.

It has been observed that volatile oils with a high specific gravity have a correspondingly low index of refraction, (McNair, 1932). If then the specific gravities of volatile oils decrease from herbs to trees, the refractive indices should increase from trees to herbs. This is the case as shown by the averages (table 2). There is chemical support, therefore, for the contention of Bessey (1915), Sinnott and Bailey (1914), and others, that in the angiosperms herbs have been derived from woody plants.

TABLE 2

Are herbs derived from trees?

HERBS	HERBS-SHRUBS	SHRUBS	SHRUB-TREES	TREES
		Alkaloids (mol. wt.)		
307	231	236	348	191
		Glycerides (iod. no.)		
117	102	96	94	66
		Volatile oils (sp. gr.)		
.8875	.9340	.9010	.9175	.8878
		Volatile oils (ref. ind.)		
1.4904	1.4918	1.4295	1.4938	1.4630

The chemical data used in table 2 are taken from McNair (1934). The following families used in the calculations are considered as consisting mainly of trees: Bombacaceae, Caricaceae, Dipterocarpaceae, Lecythidaceae, Moringaceae, Palmae, Rhizophoraceae, and Winteranaceae; the families consisting mostly of shrubs and trees are, Anacardiaceae, Anonaceae, Araliaceae, Bignoniaceae, Bixaceae, Burseraceae, Caryocaraceae, Cochlospermaceae, Combretaceae, Ebenaceae, Erythroxylaceae, Flacourtiaceae, Guttiferae, Hernandiaceae, Lauraceae, Meliaceae, Monimiaceae, Moraceae, Myristicaceae, Myrtaceae, Ochnaceae, Olacaceae, Oleaceae, Proteaceae, Salvadoraceae, Sapindaceae, Sapotaceae, Simarubiaceae, Staphyleaceae, Symplocaceae, Tiliaceae, Vochysiaceae, and Zygophyllaceae; mostly shrubs, Apocynaceae, Asclepiadaceae, Humiriaceae, Loranthaceae, and Vitaceae; the families consisting mostly of herbs, shrubs and trees, Loganiaceae, Menispermaceae, Phytolaccaceae, Rubiaceae, Sterculiaceae and Verbenaceae.

DO DICOTYLEDONS PRECEDE MONOCOTYLEDONS?

In the history of the development of taxonomic systems, there is a difference of opinion among different authors as to the precedence of the monocotyledons or the dicotyledons in the natural system. John Ray (1704), de Jussieu (1789), Eichler (1883), Engler and Prantl (1887–1909), Rendle (1925), Johnson (1931), considered monocotyledons as the antece-

dents of dicotyledons. The following botanists have believed dicotyledons to be the forbears of monocotyledons: de Candolle (1813), Bentham and Hooker (1862–1883), Wettstein (1901), Bessey (1915), Hallier (1905a, b) Clements (1914), Jeffrey (1917), Hutchinson (1926).

Bessey's (1915) phylogenetic postulate is that dicotyledons are more primitive in origin than monocotyledons. Chemical results indicate, however, that the monocotyledons precede the dicotyledons. For instance the alkaloids show by their molecular weights larger averages (table 3), e.g.

TABLE 3

Do dicotyledons precede monocotyledons?

SUB-CLASS	ALL TROPICAL FAMILIES	HERBS, HERBS-SHRUBS	SHRUBS-TREES, AND TREES
	Alkaloids (mol. wt.)		
Monocot.	230	273	144
Dicot.	306	254	222
	Glycerides (iod. no.)		
Monocot.	63.62	80.98	28.9
Dicot.	85.85	109.40	77.92
	Volatile oils (sp. gr.)		
Monocot.	.9031	.9431	.8230
Dicot.	.9166	.9118	.9179
	Volatile oils (ref. ind.)		
Monocot.	1.4739	1.4978	1.4261
Dicot.	1.4877	1.4851	1.4945

306 and 222 for the dicotyledons and respectively 230 and 144 for the monocotyledons. This is in agreement with the finding (McNair, 1934) that the more highly evolved plants produce compounds of higher molecular weights. In table 3, the iodine numbers of the glycerides are higher in the dicotyledons than in the monocotyledons, being respectively 85.85, 109.40 and 77.92 in the dicotyledons and 63.62, 80.98 and 28.90 in the monocotyledons. The specific gravities of the volatile oils (table 3) give corresponding results which are confirmed in part by the converse values of the indices of refraction.

Families in the monocotyledons and dicotyledons are given according to the Engler and Prantl system. The chemical data used are from McNair (1934). The families of the monocotyledons and dicotyledons are grouped according to the predominance in them of herbs, shrubs and trees: herbs; herbs and shrubs; shrubs and trees; and trees. The names of these families and their groupings are given above under the section, "Are herbs derived from trees?"

TABLE 4

Polypetaly versus gamopetaly

GROUP	ALL TROPICAL FAMILIES	HERBS AND HERBS-SHRUBS	SHRUBS-TREES AND TREES
	Alkaloids (mol. wt.)		
Axiflorae			
Polypet.	333	287	355
Gamopet.	308	188	0
Calyciflorae			
Polypet.	159	0	197
Gamopet.	374	0	0
	Glycerides (iod. no.)		
Axiflorae			
Polypet.	82.57	136.16	76.63
Gamopet.	84.40	103.70	70.79
Calyciflorae			
Polypet.	95.19	112.5	92.31
Gamopet.	110.77	0	0
	Volatile oils (sp. gr.)		
Axiflorae			
Polypet.	.9179	.9091	.9158
Gamopet.	.9229	.9354	0
Calyciflorae			
Polypet.	.9076	.8700	.9236
Gamopet.	.9199	0	0
	Volatile oils (ref. ind.)		
Axiflorae			
Polypet.	1.4944	1.5015	1.4961
Gamopet.	1.4815	1.4688	0
Calyciflorae			
Polypet.	1.4662	0	1.4876
Gamopet.	1.4930	0	0
	Alkaloids (mol. wt.)		
Archichlam.	298.7	287	201
Metachlam.	321	188	352
	Glycerides (iod. no.)		
Archichlam.	82.98	124.25	76.77
Metachlam.	93.84	105.48	86.82
	Volatile oils (sp. gr.)		
Archichlam.	.9150	.8960	.9179
Metachlam.	.9224	.9354	0
	Volatile oils (ref. ind.)		
Archichlam.	1.4883	1.5015	1.4944
Metachlam.	1.4853	1.4688	0

POLYPETALY VERSUS GAMOPETALY

In his consideration of flower types, Bessey (1915) considers that "Free petals (polypetaly) are more primitive than connate petals (gamopetaly)." The Bessey system divides both the axiflorae and calyciflorae into apopetalae (polypetalae) and gamopetalae. But in the Engler and Prantl classification the apopetalae are found in the archichlamydeae and the gamopetalae in the metachlamydeae.

This postulate of Bessey finds support in the chemical products of the polypetalae and gamopetalae. For instance, the glycerides (table 4) 82.57 vs. 84.40 and 95.19 vs. 110. 79; the alkaloids, 333 vs. 308, (show a difference of only 7.5%); the volatile oils give .9179 vs. .9229, 9091 vs. 9354, .9076 vs. .9199; 1.4944 vs. 1.4815, 1.5015 vs. 1.4688. In Engler and Prantl's system the archichlamydeae (apopetalae) are according to both phylogeny and chemical products more primitive than the metachlamydeae (gamopetalae). This is shown by the glycerides (table 4) 82.94 vs. 93.84, 76.77 vs. 86.82; by the alkaloids 298.7 vs. 321, and 201 vs. 352; by the volatile oils (specific gravity) .9150 vs. .9224 and .8960 vs. .9354, (refractive indices) 1.4883 vs. 1.4853 and 1.5015 vs. 1.4688.

POLYCARPY VERSUS OLIGOCARPY

Bessey (1915) advanced another postulate which finds chemical evidence in its favor. This postulate is that "many carpels (polycarpy) preceded few carpels (oligocarpy)."

TABLE 5

Polycarpy versus oligocarpy

GROUP	ALL TROPICAL FAMILIES	HERBS AND HERBS-SHRUBS	SHRUBS-TREES AND TREES
	Alkaloids (mol. wt.)		
Polycarpy	352	0	352
Dicarpy	294	188	0
	Glycerides (iod. no.)		
Polycarpy	88.04	0	88.04
Dicarpy	83.74	103.72	59.30

Bessey separates the polycarpellatae from the dicarpellatae in his gamopetalae. Chemical evidence for these divisions in the Bessey system is found only in the glycerides and the alkaloids (table 5). Neither the glycerides nor the alkaloids support the Bessey theory as shown by table 5: 88.04 versus 83.74 and 8804 versus 59.20 and 352 versus 294.

APOCARPY VERSUS SYNCARPY

In his consideration of the evolution of flower structure, Bessey (1915) states, "free carpels (apocarpy) are more primitive and from them connate carpels resulted; sometimes, however, when the carpels have remained loosely united during the evolution, they may again become quite free."

In Bessey's classification, the apopetalae have separate or united carpels, but the gamopetalae have united carpels only. Consequently, as has been shown above under "polypetaly versus gamopetaly," chemical evidence indicates that free carpels are more primitive (table 6).

TABLE 6

Apocarpy versus syncarpy

GROUP	ALL TROPICAL FAMILIES	HERBS AND HERBS-SHRUBS	SHRUBS-TREES AND TREES
	Alkaloids (mol. wt.)		
Apocarpy	333	287	355
Syncarpy (Gam.)	308	188	0
	Glycerides (iod. no.)		
Apocarpy	82.57	136.16	76.63
Syncarpy (Gam.)	84.40	103.70	70.79
	Volatile oils (sp. gr.)		
Apocarpy	.9179	.9091	.9154
Syncarpy (Gam.)	.9229	.9354	0
	Volatile oils (ref. ind.)		
Apocarpy	1.4944	1.5015	1.4961
Syncarpy (Gam.)	1.4815	1.4688	0
	Glycerides (iod. no.)		
Ranales	72.03	0	72.86
Rhoeadales	105.95	119.50	92.40

The Engler and Gilg system makes a clear separation of apocarpy from syncarpy in the Ranales (apocarpy) and Rhoeadales (syncarpy). Only glycerides have been analyzed in the Rhoeadales and no alkaloids or volatile oils. The glycerides, however, give favorable evidence to the theory e.g. (table 6) 72.03 versus 105.95 and 72.86 versus 92.40.

ENGLER AND GILG SYSTEM FROM A CHEMICAL STANDPOINT

The various divisions under the Engler and Gilg (1919) system of classification are divided for the purpose of this study into the following various sections such as the monocotyledons; A, the Amentiferae (from the Piperales to Urticales); B, Proteales to Polygonales; C, Centropermae;

D, Ranales to Umbelliflorae; A, Diapensiales to Plumbaginales; B, Ebenales; C, Contortae; and D, Tubiflorae to Campanulatae. These divisions or sections may be considered as radii originating from a central point thus forming a cart wheel design. This central point may be taken as zero and the positions of the various orders on the radii may be taken equal to the various chemical results obtained from a study of their glycerides, alkaloids, and volatile oils.

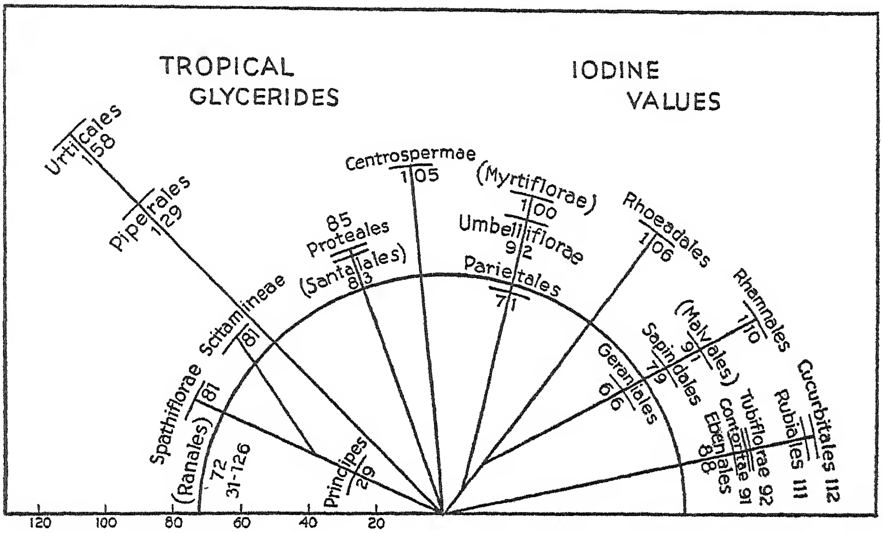

Fig. 1. A wheel-like arrangement of the orders of the Engler and Gilg system. Only those tropical orders containing glycerides are used here. The orders are placed, at distances from the axis that are equal to the average iodine absorption values of these glycerides. Each radius represents a section or branch of the Engler and Gilg phylogenetic system. Beginning from left to right there are: Monocotyledons, Amentiferae, Proteales, etc. The Ranales are represented on an arc for easy comparison with the other orders, for in the Bessey system the Ranales are the most primitive.

Glycerides. The iodine numbers of the glycerides (fig. 1) of the tropical families and sections of the Engler and Gilg system show in general a close agreement with the botanical classification. Complete agreement is found in the monocotyledonae, the amentiferae and in the metachlamydeae.

According to the Engler and Gilg phylogenetic system the Santalales are farther advanced than the Proteales. The iodine values however indicate the reverse to be true. Inasmuch as the chemical difference between them is very slight (Proteales 85 and Santalales 83) the chemical evidence is hardly sufficient to counteract the morphological evidence and phylogenetic position.

Likewise the chemical evidence here presented is probably too insignificant to warrant serious consideration for departure in phylogenetic position from Engler and Gilg classification, namely, that the Parietales 70.57 should phylogenetically precede the Ranales 72.03, or that the Geraniales 65.82 should precede the Ranales 72.03, or that the Sapindales 79.24 should precede the Malvales 90.65, or that the Umbelliflorae 91.8 should precede the Myrtiflorae 100.08.

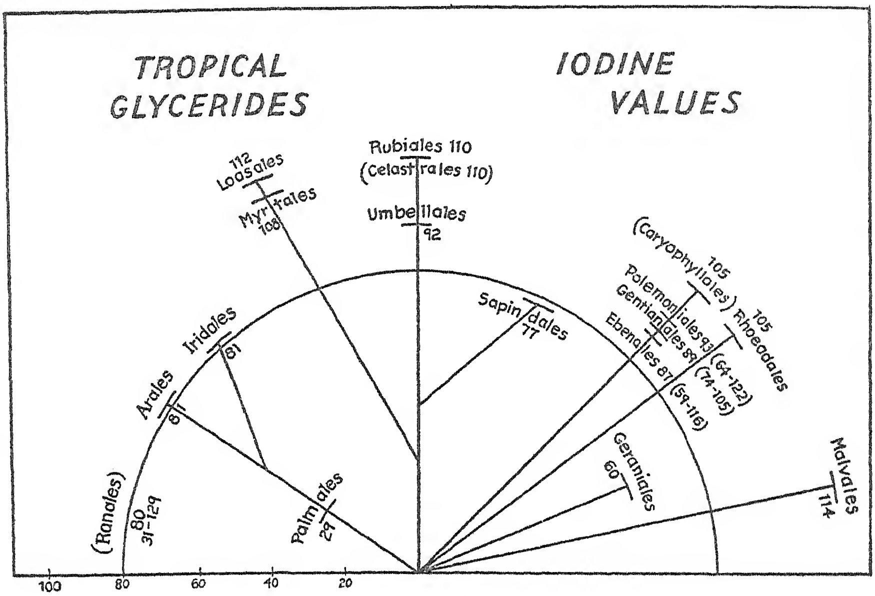

Fig. 2. A wheel-like arrangement of the orders of the Bessey system. Only those tropical orders containing glycerides are used here. The orders are placed at distances from the wheel axis that are equal to the average iodine absorption values of these glycerides. Each radius represents a section or branch of the Bessey phylogenetic system. Beginning from left to right there are the three main branches: Monocotyledoneae, Cotyloideae (cup flowers), and Strobiloideae (cone flowers).

Alkaloids. The molecular weights of the alkaloids of the tropical families and sections of the Engler and Gilg classification show in general a close agreement with the botanical classification. As in the case of the glycerides, complete agreement is found in the monocotyledonae, the amentiferae and in the metachlamydeae (except Tubiflorae). In the orders coming from the Ranales there is the usual disagreement between the Ranales and the rest of the group. The Myrtiflorae 197 are out of harmony with the Geraniales 238 and Parietales 239.

Volatile oils (*specific gravity*). The specific gravities of the volatile oils do not agree as well chemically with the Engler and Gilg botanical classification as do the glycerides and alkaloids. According to the chemical classification in the monocotyledons, the Scitamineae. 9225 precede the Spathi-

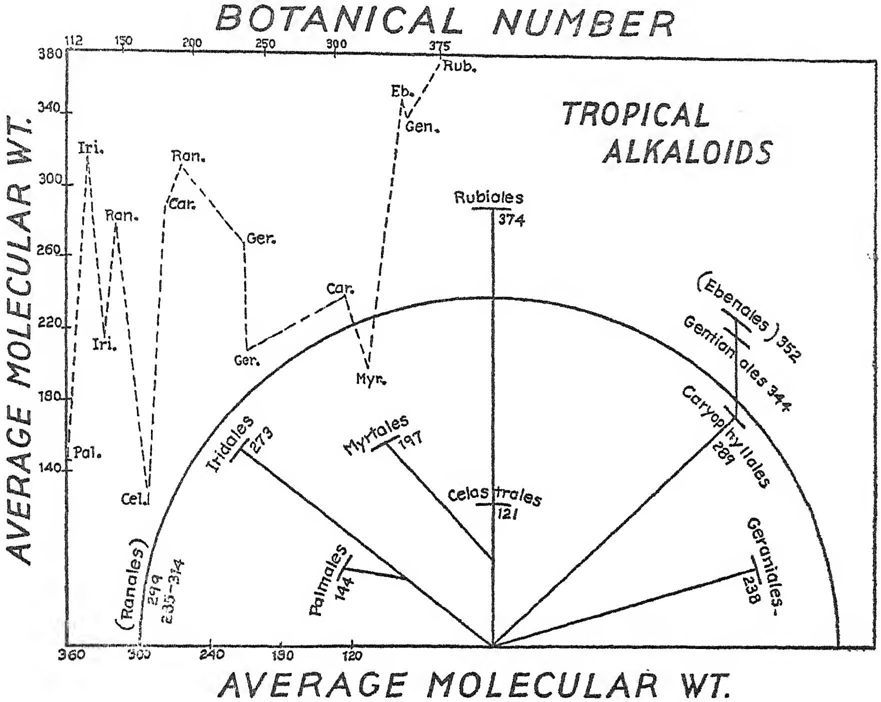

Fig. 3. A wheel-like arrangement of the orders of the Bessey system. Only those tropical orders containing alkaloids are used here. The orders are placed at distances from the wheel axis that are equal to the average molecular weights of the alkaloids of each order. Each radius represents a section or branch of the Bessey phylogenetic system. Beginning from left to right there are the three main branches: Monocotyledoneae, Cotyloideae (cup flowers), and Strobiloideae (cone flowers). The Ranales are phylogenetically at the axis or base of the Bessey system but chemically they do not so appear.

The dotted lines represent the same data that are used on the wheel. They are arranged as a polygon whose coordinates are the average molecular weights and botanical numbers of the involved alkaloids (see McNair, 1934).

florae .964, in the amentiferae the Urticales .8633 precede the Piperales .9656, and in the metachlamydeae the Tubiflorae .9309 precede the Rubiales .9199. As usual the Ranales .9324 are out of harmony with some of the group that are said to come from them, i.e. Ranales .9324 versus Rosales .8722, Geraniales .9095 and Parietales .9167.

Volatile oils (refractive index). The refractive indices furnish data which are apparently in better agreement with the Bessey system than with the Engler and Gilg classification. The Ranales are out of harmony with the Engler and Gilg system but probably in better agreement with it than with their position in the Bessey system. The Piperales are not in harmony with the Urticales, the Rhamnales are out of position in regard to the Sapindales and Malvales, and the Geraniales are out of their proper systematic position in relation to the Sapindales, Malvales and Rhamnales.

THE BESSEY SYSTEM FROM A CHEMICAL STANDPOINT

The Bessey system (1914), like the Engler and Gilg, recognizes the two main divisions of monocotyledons and dicotyledons. The dicotyledons, however, are divided differently than in the Engler and Gilg. Bessey divides them into axiflorae and calyciflorae. In the axiflorae "axis flowers," the axis of the flower is normally cylindrical, spherical, hemispherical or flattened, bearing on its surface the hypogynous perianth, stamens and carpels (or the stamens may be attached to the corolla). In the calyciflorae, "cup flowers," the axis of the flower is normally expanded into a disk or cup, bearing on its margin the perianth and stamens (or the latter may be attached to the corolla). The axiflorae are considered as more primitive.

The groups of the Bessey system may be considered as radii originating from a central point. This central point may be taken as zero and the positions of the various orders on the radii may be taken as the various chemical results obtained from a study of their glycerides, alkaloids and volatile oils.

Glycerides. The iodine numbers of the glycerides (fig. 2) of the tropical families and sections of the Bessey system show in general a close agreement with the botanical classification. Only three of the orders do not agree with the botanical classification, viz., the Caryophyllales, Celastrales and Ranales. The Caryophyllales 105 should precede the Ebenales 87. The Celastrales 110 should precede the Umbellales 92. The Ranales 80 should be nearer the point of origin than any of the other dicotyledons.

Alkaloids. The molecular weights of the alkaloids (fig. 3) of the tropical families and sections of the Bessey classification show in general a close agreement with the botanical classification. But two discrepancies are noted. The Ranales 299 should precede all other dicotyledons, i.e. in this case they should have a lower number than 121. The Ebenales 352 should precede the Gentianales 344.

Volatile oils (specific gravity). Only one inharmonious order is found in this arrangement (fig. 4) and that is the usual case of the Ranales. The

Ranales .9308 should come before any of the rest of the dicotyledons, i.e., should have a lower number than .8722.

Volatile oils (refractive indices). As in the case of the specific gravities of the volatile oils, the Ranales are alone in not being in agreement with the botanical classification (fig. 5). The Ranales 1.5013 should be less than 1.429.

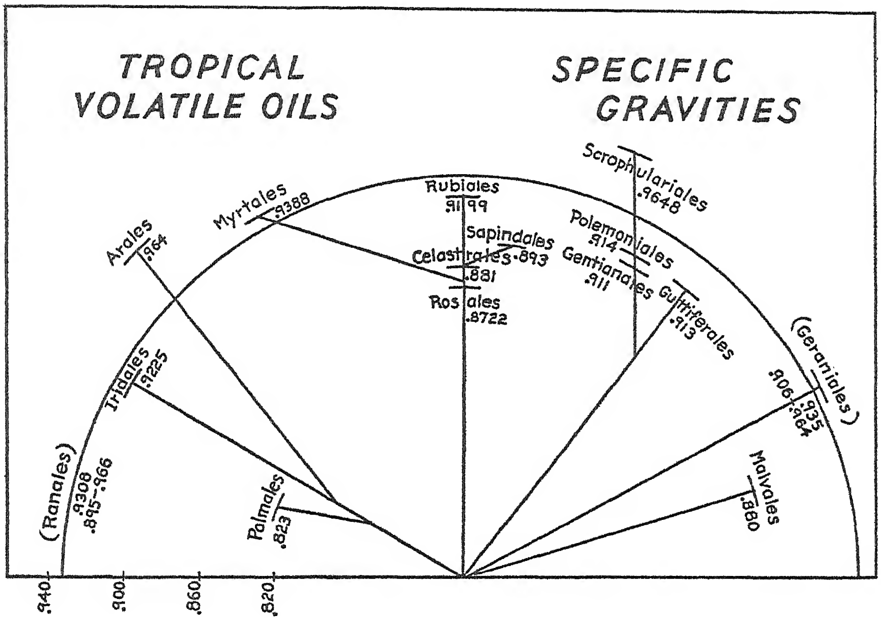

Fig. 4. A wheel-like arrangement of the orders of the Bessey system. Only those tropical orders containing volatile oils whose specific gravities have been determined are used here. The orders are placed at distances from the wheel axis equal to the average specific gravities of the volatile oils of each order. Each radius represents a section or branch of the Bessey phylogenetic system, beginning from left to right there are the three main branches: Monocotyledoneae, Cotyloideae (cup flowers), and Strobiloideae (cone flowers). The Ranales phylogenetically at the base or axis of the Bessey system are represented as on an arc and chemically not at the axis of the system.

DISCUSSION OF THE ENGLER AND GILG AND BESSEY SYSTEMS FROM A CHEMICAL POINT OF VIEW

The Engler and Gilg system considers that monocotyledons precede dicotyledons. The Bessey system on the contrary classes dicotyledons as coming before monocotyledons. The chemical evidence given in this paper supports the Engler and Gilg contention: that monocotyledons may have preceded dicotyledons (table 3).

With this exception both systems agree in their use of the following phylogenetic principles:

1. Polypetalous flowers are more primitive than gamopetalous ones.
2. Numerous carpels represent a more primitive condition than few carpels.
3. Separate carpels represent a more primitive condition than united carpels.

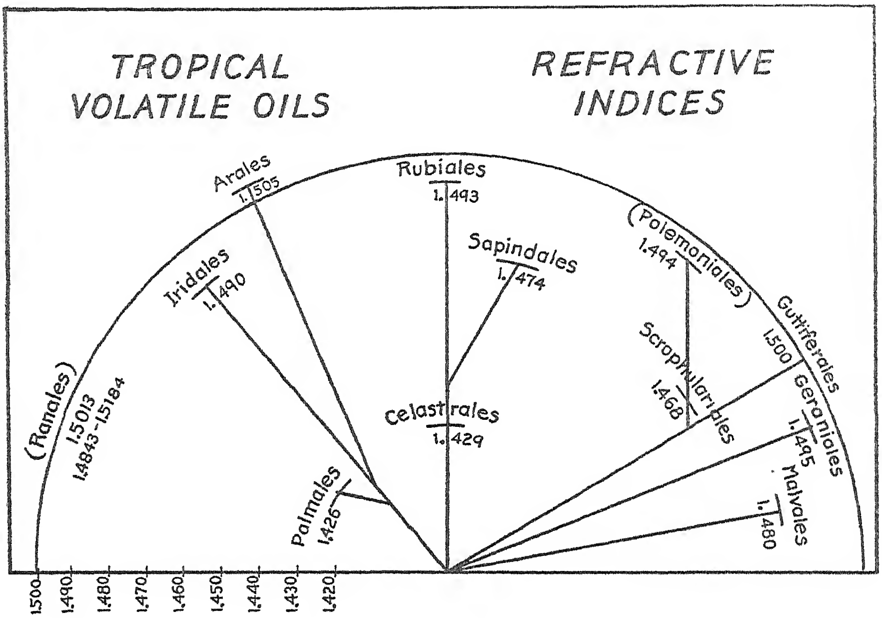

Fig. 5. A wheel-like arrangement of the orders of the Bessey system. Only those tropical orders containing volatile oils whose refractive indices have been determined are used here. The orders are placed at distances from the wheel axis equal to the average refractive indices of the volatile oils of each order. Each "spoke" or radius with its connections (arms) represents a branch of the phylogenetic tree of Bessey. Beginning from left to right there are the three main branches: Monocotyledoneae, Cotyloideae (cup flowers), and Strobiloidae (cone flowers). If one looked down upon a tree from its top the branches would appear to radiate from a common center. In a similar way the branches of the phylogenetic tree are here presented.

All of these, except no. 2, have been shown to hold true from the chemical investigations. In this case chemical evidence (table 5) indicates that few carpels may represent a more primitive condition than many carpels. The Bessey, and the Engler and Gilg systems, however, differ in the relative importance given to these phylogenetic principles.

In both systems the Ranales do not fall in the position allotted to them.

There is, however, better agreement with their position in the Engler and Gilg system than with their position in the Bessey system.

The Ebenales and Gentianales are out of harmony in the Bessey system (alkaloids, fig. 3). These are closer together in the Engler and Gilg system.

The Caryophyllales and Gentianales are far removed in the Engler and Gilg but may agree better with that classification than with Bessey's (glycerides, fig. 1).

The Celastrales and Umbellales do not harmonize with the Bessey system (glycerides, fig. 2). These are in better accord in Engler and Gilg.

PROTEINS VERSUS ALKALOIDS, GLYCERIDES AND VOLATILE OILS AS PLANT DETERMINANTS

Mez (1922, 1926) in his serum diagnostic method for determining plant relationship, makes use of protein plant constituents. The Moyer (1934) electrophoretic method also depends upon proteins for its usefulness. Both of these methods give serial plant sequences in plant classification, but do not show the relative evolutionary development of various plant groups, e.g. the palms versus the iris, or the palms versus the Rubiales. The use of the molecular weights of the alkaloids, of the iodine numbers of the glycerides, of the specific gravities or refractive indices of volatile oils give numerical values for plant groups, and in this way more definite comparative values for evolutionary appreciation are determined. For instance, the iodine numbers of the glycerides give for the palms (Principes or Palmales) 29, the iris (Liliiflorae or Iridales) 81, and the Rubiales 111. From these results the palms are the most primitive, the iris next and the Rubiales the most developed. The Rubiales may perhaps be considered as having developed four times farther than the palms, at least in their ability to produce unsaturated glycerides.

The use of proteins in plant determination requires the use of fresh material. This is often difficult to obtain for some groups. The use of alkaloids, glycerides and volatile oils does not require fresh material and thus has the advantage over the use of proteins.

SUMMARY

Some of the chemical products produced by plants are influenced by the climate in which they are formed. Fats (glycerides) produced in the tropics have lower iodine values than fats formed in temperate regions. Alkaloids found in tropical plant families have smaller molecular weights than those of the temperate regions. Volatile (essential) oils have lower specific gravities and higher refractive indices when formed in the tropics than when formed in a temperate climate. In other words it would seem

that more complex chemical products are formed in the temperate regions than are formed in the tropics.

When these three classes of substances appear in plants of the same climatic zone, e.g., in the tropics, the chemical properties vary with the degree of evolution of the plant according to the Engler and Gilg system. The highest evolved fats have the highest iodine values, the highest evolved alkaloids have the largest molecular weights, and the highest evolved volatile oils have the greatest specific gravities as well as the lowest refractive indices.

According to evidence obtained from the analyses of alkaloids, glycerides, and volatile oils formed by plants:

The Ranunculaceae may have been preceded by the Berberidaceae and Lardizabalaceae.

Herbs may have been derived from trees.

Monocotyledons may have preceded dicotyledons.

Free petal flowers (polypetaly) are more primitive than united petal flowers (gamopetaly).

Few carpels (oligocarpy) preceded many carpels (polycarpy).

Free carpels (apocarpy) may be more primitive than united carpels (syncarpy or gamocarpy).

These chemical findings may be used in comparing various systems of plant classification, e.g., the Bessey and the Engler and Gilg systems. The Bessey system considers dicotyledons as more primitive than monocotyledons. Chemical evidence does not support this view, but favors in this regard the Engler and Gilg classification. The other phylogenetic principles as listed in the preceding paragraph are used in both systems, although both consider many carpels more primitive than few carpels.

In both systems, according to the chemical evidence, the Ranales do not fall in the positions allotted to them. There is, however, better agreement with their position in the Engler and Gilg system.

The Ebenales and Gentianales are out of harmony in the Bessey system. These are closer together (both in Contortae) in the Engler and Gilg system.

The Caryophyllales and Gentianales of Bessey are far removed in the Engler and Gilg (being respectively Myrtiflorae and Contortae), and the chemical findings may agree better with that classification than with Bessey's.

The Celastrales and Umbellales do not harmonize with the Bessey system. These are in better accord with Engler and Gilg where the orders are considered as Sapindales and Umbelliflorae.

In the taxonomic revision of various plant groups, the serum diagnostic

method of Mez and the electrophoretic method of Moyer may give correct taxonomic sequences, but the use of alkaloids, glycerides and volatile oils gives not only these sequences but also (because they deal in numerical values) gives an idea as to the relative degree in evolution of various groups e.g. the palms versus the iris, or the palms versus the Rubiales.

The methods of Mez and Moyer require fresh material, while the alkaloids, etc., may be obtained from dried herbarium materials.

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The Nipissing flora of the Apostle Islands region

L. R. Wilson

In Science, February 13, 1931, a fossil flora of the Nipissing Great Lakes was briefly described by the writer. As was there stated, the plant remains are preserved in the form of rather extensive peat beds submerged in Lake Superior in the vicinity of the Apostle Islands, Bayfield County, Wisconsin. The samples, sent by Prof. J. A. Merrill, of the Superior State Teachers College, were recovered from beneath fourteen feet of sand and forty feet of water about one and one-half miles west of Sand Island, Bayfield County, Wisconsin. The geological significance of this deposit has been discussed by Dr. F. B. Taylor (Science **74**: 265–267, 1931.) and the formation of the peat set as contemporaneous with the original one-outlet stage of the Nipissing Great Lakes.

The botanical importance of this deposit becomes evident when one reviews literature dealing with the plant life associated with the Glacial Great Lakes. Two facts stand out, particularly: that the actual knowledge of the plants occurring at this period in the history of the Great Lakes is confined to one or more species of *Chara* (Coleman, A. P., Toronto University Studies, Biol. Sur. No. 21; 1922), and that much hypothetical dating of the appearance of certain Atlantic Coastal Plain plants and others in the upper Great Lakes Region, has been done, based entirely upon an interpretation of their present distribution (Peattie, D. C., Rhodora **24**: 57–70, 80–88; 1922., McLaughlin, W. T., Ecol. Mon. **2**: 335–383; 1932, and Anderson, E., Rhodora **35**: 154–160; 1933). The appearance of these Coastal Plain plants in the Great Lakes Region at an early post glacial date seems very probable, but only since the discovery of the submerged peat beds in Lake Superior is it possible to reconstruct a picture of the ecological conditions of early Glacial Lake Nipissing time and to state definitely what plants then existed in northern Wisconsin.

An examination of the largest sample of peat, which is approximately eighteen inches square and four inches thick, shows that it is of a type formed in comparatively still shallow water. About one-half of the thickness of the sample is made up of organic mud, throughout which occur fragments of plant and animal tissues. This portion of the sample is evidently a deeper water deposit than the other half which contains organic tissues in greater abundance and perfection. It seems reasonable to consider the latter as the upper side, but considering the history of the region it is impossible to state definitely.

The largest sample was separated arbitrarily into three horizons, and examined both macro- and microscopically for fossils. The horizon con-

taining the greatest percentage of organic mud and little plant tissue, is horizon No. 1, the middle horizon is No. 2, and that containing much tissue and little organic mud is No. 3.

The families, genera, and species of plants that have been recognized as fossils in the peat are listed below with their stratigraphic position. A pollen spectrum of the three horizons was also attempted and the table below is based on a count of one thousand fossils from each level.

Flora of the Nipissing peat

Sphagnum sp. (spores; in No. 3, stems and leaves) general.
Polypodiaceae sp. (spores) No. 3.
Lycopodium clavatum (spores) No. 1.
Taxus canadensis (wood) No. 1.
Pinus Strobus (pollen; in No. 1, cone) general.
P. Banksiana (pollen) general.
P. resinosa (pollen) general.
Larix laricina (pollen) No. 3.
Picea mariana (pollen) general.
Abies balsamea (pollen; in No. 1, cone scale) general.
Gramineae (pollen) general.
Cyperaceae (pollen) No. 1.
Carex crinita (leaves, rhizomes and possibly an achene of this species) Nos. 2 and 3. The distinctive markings on the sheaths made the identification of this species certain.
Salix sp. (pollen) No. 2.
Betula papyrifera (pollen) general.
B. pumila (pollen) general.
Alnus sp. (pollen) No. 1.
Quercus sp. (pollen) Nos. 1 and 2.
Acer spicatum (pollen) general.
Ericaceae (pollen of two genera) general.
Chamaedaphne calyculata (trichomes and leaves) general.
Compositae (pollen of four genera) general.

Percentage of microfossils in the Nipissing peat

SPECIES	HORIZON (1)	(2)	(3)
Sphagnum	1.4	34.2	16.0
Polypodiaceae	0.0	0.0	0.7
Lycopodium clavatum	0.5	0.0	0.0
Pinus resinosa and *P. Strobus*	16.6	8.3	34.1
P. Banksiana	7.2	14.4	17.0
Picea	45.3	6.0	16.1
Abies	9.5	4.1	4.2
Gramineae	5.4	2.4	1.4

Cyperaceae	0.6	0.0	0.0
Betula	10.1	24.1	6.0
Alnus	0.3	0.0	0.0
Quercus	1.1	0.6	0.0
Acer	0.4	0.4	0.5
Ericaceae	0.6	0.5	2.3
Compositae	1.0	5.0	1.7

An examination of the species recognized from the peat shows that they are typical of the Canadian Zone. Other studies upon peat deposits of pro- and post-Glacial Lake Nipissing age in northern Wisconsin (paper in preparation) show that there was a definite plant succession upon the area uncovered by the water in its drop from the Algonquin level to that of the Nipissing. This recorded succession in the peat deposits begins with an almost total percent of *Picea* and a small percent of *Pinus*. Slightly higher in the profiles, other components of the present flora appear. An unsuccessful attempt was made to fit the spectrum of the Nipissing peat into those of the other deposits studied. In spite of this it is definite that the Nipissing material does not record the pioneer vegetation of the region, and that the bottom layers of the submerged peat deposit were not collected. The species represented as fossils suggest that before the close of the one-outlet stage of Glacial Lake Nipissing, sufficient time had elapsed to allow the succession of plant communities to go far beyond the pioneer stage. For the development of a plant community, such as suggested by the fossils, several centuries, if not longer, must have elapsed.

The writer is indebted to Prof. J. A. Merrill, for the opportunity of examining this valuable deposit and to Dr. N. C. Fassett, of the Department of Botany, University of Wisconsin, for helpful criticism during the investigation.

COE COLLEGE,
CEDAR RAPIDS, IOWA

Euphorbia capitellata, its synonymy and range

Louis C. Wheeler

Euphorbia capitellata Engelm. ex Torr., Bot. Mex. Bound. 188. 1859.

Chamaesyce capitellata (Engelm.) Millsp., Field Mus. Pub. Bot. **2**: 408. 1916.

Euphorbia pycnanthema Engelm. ex Torr., Bot. Mex. Bound. 188. 1859.

Chamaesyce pycnanthema (Engelm.) Millsp., Field Mus. Pub. Bot. **2**: 411. 1916.

Euphorbia Chamberlinii Johnston, Proc. Cal. Acad. Sci. IV; **12**: 1066. 1924.

Euphorbia capitellata is extremely variable; habit from prostrate to erect; vesture from nearly glabrous to densely short pubescent; leaf shape from ovate to narrowly linear-lanceolate; leaf margin from entire to coarsely serrate. The most strikingly characteristic feature of this species is the bearing of the involucres in small heads but this character alone will not distinguish the species from some other Anisophyllae.

Examination of about a hundred sheets of this species from various herbaria has convinced me that only one species can be recognized even though it is a polymorphic entity. Also I have compared fragments (from the Field Museum, Chicago) of the types of *Euphorbia capitellata* and *E. pycnanthema* and they seem to be identical. It is interesting that Engelmann in the original description (q.v.) expressed a doubt that the two are distinct. The only definite difference in the two descriptions is that *E. capitellata* is annual and *E. pycnanthema* perennial. As the perennial members of *Euphorbia*, section Anisophyllum, subsection Chamaesyce bloom the first year it is impossible, with only one specimen, to be sure a species is annual. *E. capitellata* is the valid name by priority of position.

I have examined the type of *Euphorbia Chamberlinii* Johnston and it does not differ essentially from typical *E. capitellata*. The leaves are entire nearly throughout but many other specimens of *E. capitellata* have entire leaves. The type of *E. Chamberlinii* is heavily parasitized with white coccids which gives it a confusing appearance.

Euphorbia capitellata ranges from southern Arizona south into Lower California, Sonora, and Sinaloa, and east through Chihuahua and Coahuila. There is one collection doubtfully from California. See Bull. So. Cal. Acad. Sci. **31**: 105. 1934 for discussion of this.

Euphorbia capitellata Engelm. var. laxiflora Wats., Proc. Am. Acad. **24**: 74. 1889.

Euphorbia gladiosa Jones, Con. West. Bot. **15:** 144. 1929. I have seen the type of *E. gladiosa* at Pomona College Herbarium and it is in no respect different. This variety is distinguished from the typical species by the very lax habit and the narrowly linear-lanceolate leaves. It is local about Guaymas, Sonora.

LA VERNE, CAL.

INDEX TO AMERICAN BOTANICAL LITERATURE

1931–1935

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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